ISSN 1014-5602

FAO Fisheries Synopsis No. 156 FIR/S156

SAST - European Abalone 3,07(03)001,14

SYNOPSIS OF BIOLOGICAL DATA ON THE EUROPEAN ABALONE (ORMER) *Haliotis tuberculata* LINNAEUS, 1758 (GASTROPODA: HALIOTIDAE)

LIBRARY

DEC 13 1995

National Marine Fisheries Service
2570 Dole Street
Honolulu, Hawaii

Food and Agriculture Organization of the United Nations

FAO
fish.
synop.
no. 156

SYNOPSIS OF BIOLOGICAL DATA ON THE EUROPEAN ABALONE (ORMER), *Haliotis tuberculata* LINNAEUS, 1758 (GASTROPODA: HALIOTIDAE)

Prepared by

Yunus D. Mgaya*
University of Dar es Salaam
Department of Zoology and Marine Biology
P. O. Box 35064, Dar es Salaam
Tanzania

LIBRARY

DEC 1 3 1995

National Marine Fisheries Service
2570 Dole Street
Honolulu, Hawaii

* Present address:
University College Galway
Shellfish Research Laboratory
Carna, Co. Galway
Ireland

FAO
fish.
synop.
no 156

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1995

The designations employed and the presentation of material in this publication do not imply the expression of any opinion whatsoever on the part of the Food and Agriculture Organization of the United Nations concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries.

M-42
ISBN 92-5-103694-2

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying or otherwise, without the prior permission of the copyright owner. Applications for such permission, with a statement of the purpose and extent of the reproduction, should be addressed to the Director, Publications Division, Food and Agriculture Organization of the United Nations, Viale delle Terme di Caracalla, 00100 Rome, Italy.

© FAO 1995

PREPARATION OF THIS SYNOPSIS

The present review concerns the biology, fisheries and cultivation of the European abalone (ormer), *Haliotis tuberculata* (L.), a gastropod mollusc which inhabits the Atlantic coast from the south of the English Channel down to the northwest coast of Africa. The ormer is a greatly prized species in the British Channel Islands and in France, especially the Brittany area, where a fishery exists.

Overexploitation of intertidal ormer populations has led to imposition of a ban on ormer fishing, for example, between 1974 and 1976 an official ban was imposed in the Channel Island of Guernsey. Against this background and the fact that the abalone world market is quite buoyant, cultivation of the species has been an attractive proposition and is currently underway in several places, notably Ireland, the Channel Isles, and France. As quantitative and qualitative information of various aspects of the biology, ecology, stocks, and cultivation of *H. tuberculata* is widely scattered in the literature, this review was undertaken to serve as a compendium of knowledge on this important mollusc.

ACKNOWLEDGEMENTS

I am greatly indebted to Kent E. Carpenter of FAO, Rome, for encouragement to write this synopsis. I would like to express sincere gratitude to Dr. John P. Mercer and the staff of the Shellfish Research Laboratory, University College Galway for their valuable support and interest in this work. Special thanks are due to the staff of the James Hardiman Library of the University College Galway for helping to obtain many papers through the interlibrary loan service. The help of Steven Ozanne of the Guernsey Sea Fisheries Committee who supplied ormer landing statistics is gratefully acknowledged. For the translation of a number of French papers, I am grateful to Antoine Pennec and Conor Pyle. Thanks are also due to Drs W. A. Crowe, T. W. Burke and Mr. Kangsen Mai for their constructive criticism of the manuscript and helpful suggestions. Finally I wish to extend my deepest appreciation to all the people whose names could not be listed here but provided help towards the completion of this review. The work has been made possible by a postgraduate research studentship from the Government of the Republic of Ireland.

J.-M. Poutiers, Muséum National d'Histoire Naturelle, Paris, reviewed the manuscript and made many valuable suggestions. G. Sciarappa-Demuro, FAO, Rome, completed page composition and layout.

Mgaya, Y.D.

Synopsis of biological data on the European abalone (ormer), *Haliotis tuberculata* Linnaeus, 1758 (Gastropoda: Haliotidae)

FAO Fisheries Synopsis. No. 156. Rome, FAO. 1995. 28p.

ABSTRACT

This synopsis compiles and reviews the currently available information on the biology, fisheries and cultivation of the ormer, *Haliotis tuberculata*. Topics include taxonomy, morphology, distribution, reproduction, pre-adult and adult stages, food and feeding, growth, movement, population characteristics, and various aspects of exploitation and culture. Data and information were obtained from both the more formal scientific publications as well as less formal journals, newsletters, regular reports and theses, as acknowledged in the text.

Distribution:
Author
FAO Fisheries Officer
Regional Fisheries Councils and Commissions
Selector SC

CONTENTS

Page

1. IDENTITY 1
   1.1 Nomenclature 1
      1.1.1 Valid scientific name 1
      1.1.2 Synonymy 1
   1.2 Taxonomy 1
      1.2.1 Affinities 1
         1.2.1.1 Suprageneric 1
         1.2.1.2 Generic 1
         1.2.1.3 Specific 2
      1.2.2 Taxonomic status 2
      1.2.3 Subspecies 2
      1.2.4 Standard common names, vernacular names 2
   1.3 Morphology 3
      1.3.1 External morphology 3
      1.3.2 Cytomorphology 4

2. DISTRIBUTION 4
   2.1 Total area 4
   2.2 Differential distribution 4
      2.2.1 Spawn, larvae, and juveniles 4
      2.2.2 Adults 5
   2.3 Determinants of distribution changes 5
      2.3.1 Temperature 5
      2.3.2 Salinity 5
      2.3.3 Currents and wave surge 5
      2.3.4 Food 5
      2.3.5 Habitat 5
      2.3.6 Behavioural adaptation 5
   2.4 Hybridization 5

3. BIONOMICS AND LIFE HISTORY 6
   3.1 Reproduction 6
      3.1.1 Sexuality 6
      3.1.2 Maturity 6
      3.1.3 Mating 6
      3.1.4 Fertilization 6
      3.1.5 Gonads 6
      3.1.6 Spawning 6
      3.1.7 Spawn 7

Page

3.2 Pre-adult phase . . . 7
3.2.1 Embryonic phase . . . 7
3.2.2 Larval and early juvenile phase . . . 7
3.2.3 Juvenile phase . . . 10
3.3 Adult phase . . . 10
3.3.1 Longevity . . . 10
3.3.2 Hardiness . . . 10
3.3.3 Competitors . . . 10
3.3.4 Predators . . . 10
3.3.5 Parasites, diseases, injuries and abnormalities . . . 11
3.3.6 Chemical composition . . . 11
3.4 Nutrition and growth . . . 11
3.4.1 Feeding . . . 11
3.4.2 Food . . . 12
3.4.3 Growth rate . . . 12
3.4.4 Metabolism . . . 14
3.5 Behaviour . . . 14
3.5.1 Migrations and local movements . . . 14
3.5.2 Schooling . . . 15
3.5.3 Responses to stimuli . . . 15

4 POPULATION . . . 15
4.1 Structure . . . 15
4.1.1 Sex ratio . . . 15
4.1.2 Age composition . . . 15
4.1.3 Size composition . . . 15
4.2 Abundance and density . . . 17
4.3 Natality and recruitment . . . 18
4.3.1 Reproduction rates . . . 18
4.3.2 Factors affecting reproduction . . . 18
4.3.3 Recruitment . . . 18
4.4 Mortality and morbidity . . . 18
4.4.1 Mortality rates . . . 18
4.4.2 Factors causing or affecting mortality . . . 18
4.4.3 Factors affecting morbidity . . . 18

5 EXPLOITATION . . . 18
5.1 Fishing equipment . . . 18
5.1.1 Gears . . . 18
5.1.2 Boats . . . 19

Page

5.2 Fishing areas 19
5.2.1 General geographic distribution 19
5.2.2 Geographic ranges 19
5.2.3 Depth ranges 19
5.2.4 Conditions of the grounds 19
5.3 Fishing seasons 19
5.4 Fishing operations and results 19
5.4.1 Effort and intensity 19
5.4.2 Selectivity 19
5.4.3 Catches 19

6. PROTECTION AND MANAGEMENT 20
6.1 Regulatory (legislative) measures 20
6.1.1 Limitation or reduction of total catch 20
6.1.2 Protection of portions of population 20

7. CULTURE 20
7.1 Procurement of stocks 20
7.2 Genetic selection of stocks 20
7.3 Induction of spawning and fertilization 20
7.4 Rearing 21

8. REFERENCES 23

1. IDENTITY

1.1 Nomenclature

1.1.1 Valid scientific names

First taxonomically valid description of ***Haliotis tuberculata*** L. appeared in 1758 in the 10th edition of Systema Naturae (Linnaeus, 1758): p. 1256 with ***Haliotis asinina*** Linnaeus as the type species by subsequent designation (Montfort, 1810).

1.1.2 Synonymy

The following synonymy is based on the works of Wagner and Abbott (1978) and Lindberg (1992):

Haliotis adriatica Nardo, 1847, Sin. mod. spec. Lag. Veneto, p. 97

Haliotis bistriata Gmelin, 1791, *Syst. Nat. Linn.*, Ed. XIII, p. 3689

Haliotis incisa Reeve, 1846, Conch. Icon., Vol. III, pl. 15 fig. 57

Haliotis lamellosa Lamarck, 1822, Anim. sans Vert., t. VI, 2^{e} part., p. 217

Haliotis lucida Requien, 1848, Cat. Coq. Corse, p. 62

Haliotis pellucida von Salis, 1793, Reise Neapel, p. 380

Haliotis reticulata Reeve, 1846, Conch. Icon., Vol. III, pl. 14 fig. 48

Haliotis rugosa Lamarck, 1822, Anim. sans Vert., t. VI, 2^{e} part., p. 217

Haliotis vulgaris da Costa, 1778, Brit. Conch., Vol. 2, fig. 1-2

1.2 Taxonomy

1.2.1 Affinities

1.2.1.1 Suprageneric

The classification here adopted is that used by Vaught (1989):

Phylum Mollusca Linnaeus, 1758

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia H.-M. Edwards, 1848

Order Archaeogastropoda Thiele, 1929

Superfamily Pleurotomarioidea Swainson, 1840

Family Haliotidae Rafinesque, 1815

The following description of family Haliotidae is adapted from Thiele (1929):

Shell nacreous internally, coloured externally; ear-shaped, with few rapidly-increasing whorls, which are open below, so that one can see the entire inner side up to the tip. Columella absent, the margin below is only somewhat bent in. Spire variable in size, generally small in comparison with the extensive last whorl. At the outer side of the whorls, with the exception of the first 2, there is a series of holes, in most cases with raised margins, some of which close to the shell aperture are open; the others are closed.

Animal with a broad oval foot, without operculum; above it and below the mantle, a very strongly developed epipodium is present, which ends anteriorly at the head tentacles and consists of a strong fold with numerous somewhat branched processes and tentacles; above and lateral to the head tentacles there are shorter processes with the open eyes, joined with the lobed margin by an integumental fold. Mantle deeply cleft, corresponding to the series of holes; along the margins of the cleft there are three tentacles which protrude out through the holes in the shell. Mantle cavity very deep, shifted toward the left, with 2 bipectinate gills, on the axis of which a sensory band represents the osphradium. Between the gills open the hind gut and the two kidneys connected with the pericardium consisting of a ventricle, which is penetrated by the hindgut, and 2 auricles. Gonad opening into the outer part of the right kidney. Mouth opening in a short snout. Radula of rhipidoglossate type: central tooth broad and fairly short, with simple broad cutting edge; on either side of it are lateral teeth, the first of similar size to the central tooth, somewhat obliquely directed forward, usually with rounded cutting edge; the second obliquely turned backward with pointed or rounded cutting edge; the 3 following teeth have very strong pointed cutting edges; the innermost of these is the narrowest, the outermost the widest. The numerous identical marginal teeth possess rounded cutting edges, denticulate on the sides. A pair of salivary glands cutting open into the oral cavity. Oesophagus with a pair of glandular sacks with villous epithelial processes. Stomach in 3 or 4 parts, with spirally-coiled blind sac. Intestine forming long forwardly-turned loop and opening into the mantle cavity between the gills.

Nervous system with an oesophageal ring in the head, of which the lateral swellings constitute the cerebral ganglia. In the foot, long nerve cords connected like a ladder, from the anterior ends of which the ganglionicly twisted visceral commissure arises. Cerebral ganglia joined with the pedal cords each by 2 connectives. A nerve network in the epipodium, connected with the pedal cords by several transverse connectives. Buccal connectives arising from the labial commissure. A small muscle present on the left side, in addition to the enormous muscular mass situated to the right of the gill cavity, which corresponds to the columellar muscle.

1.2.1.2 Generic

Genus ***Haliotis*** Linnaeus, 1758. This is the only genus currently recognized within the family Haliotidae. However, a number of subgeneric taxa have been proposed, based mainly on conchological characters, some of them being elevated to full generic rank by Australian or Japanese authors (For a review of generic taxa, see Cox, 1960). As their phylogenetic value has not been established (Lindberg, 1992), they will not be diagnosed here.

Haliotis tuberculata was assigned to subgenus ***Sulculus*** Adams and Adams, 1854 (Cox, 1960) or to ***Euhaliotis*** Wenz, 1938 (Nordsieck, 1968). It has been made by original designation the type-species of genus ***Eurotis*** by Habe and Kosuge (1964), but this also has not received general acceptance among workers.

1.2.1.3 Specific

The following diagnosis of ***Haliotis tuberculata*** is from Graham (1988): "Shell ear-shaped with very low spire; 5-7 small openings with out-turned lips lie in spiral along the last whorl and are continued up the spire as a series of closed tubercles. Aperture very large; inside of shell with bright mother-of-pearl sheen. Foot without an operculum. The shell has 3-4 rapidly expanding whorls marked with many fine spiral lines. The aperture is oval, the outer lip with a sharp edge, the inner lip turned inwards to form a narrow shelf. Pinkish when young with light and dark mottling or bars; older shells are darker, reddish brown or greenish. The head is small and flattened, carrying two long tentacles each with a bluish eye on a stalk on the outer side of its base. Cephalic lappets form a fold across the head dorsal to the tentacles. The mantle edge is thickened and warty and slit under the row of holes in the shell. The foot is large and powerful, with an oval sole; its sides are papillated ventrally and carry a thick epipodial ridge dorsally which has a scalloped edge. Many tentacles project from between the lobes. The posterior end of the foot bears transverse ridges and grooves on its dorsal surface. Brown or greenish, with darker and lighter blotches, sometimes alternating to give stripes on the epipodium."

1.2.2 Taxonomic status

Haliotis tuberculata is the only species in the family Haliotidae which is harvested commercially in Europe. Wagner and Abbott (1978), and Abbott and Dance (1982) consider ***H. lamellosa*** a subspecies or form of ***H. tuberculata***. Based on the morphology of the radulae of ***H. tuberculata*** and ***H. lamellosa***, Gaillard (1958) was first of the opinion that ***H. lamellosa*** is not a separate species but rather a variety of ***H. tuberculata***. Later, following Bruschi et al. (1985), he considered ***H. lamellosa*** a subspecies of ***H. tuberculata*** (Gaillard, 1987). Since Bucquoy et al. (1886) first expressed the idea in detail, a number of authors claim that ***H. lamellosa*** represents a distinct, mainly Mediterranean species (Garavelli, 1968a, b; D'Angelo and Gargiullo, 1978; Nordsieck, 1982; Barash and Danin, 1992).

Colombera and Tagliaferri (1983) found the number and morphology of chromosomes of ***H. tuberculata*** and ***H. lamellosa*** to be similar. However, the problem of the status of ***H. lamellosa*** remains open, as much still remains to be investigated concerning its relationships with ***H. tuberculata*** by breeding experiments, comparative studies using enzyme electrophoresis, DNA sequencing, or multivariate techniques applied to both enzyme and morphometric phenotypes.

1.2.3 Subspecies

Full specific synonymies for ***Haliotis lamellosa*** Lamarck, 1822 were given by Bucquoy et al. (1886), Pilsbry (1890), and Sabelli et al. (1990-1992).

As discussed above, the authors do not agree whether the Mediterranean populations of ormer should be considered a different species, a subspecies or a simple form of ***H. tuberculata***. It is not the task of the present author to argue for, or against, the use of ***lamellosa*** in one of these three cases. Instead, an attempt is made to clarify the phenotypic distinction of ***H. tuberculata*** *s.s.* and ***H. t. lamellosa*** with a key (translated from Poutiers, 1993) and illustrations (from Gaillard, 1987):

- Shell relatively large, rounded oval in outline. External surface with rather shallow radial undulations (**Figure 1a**) ..... ***Haliotis tuberculata tuberculata***
- Shell relatively small, elongated oval in outline. External surface with strong, irregular radial folds (**Figure 1b**)..... ***Haliotis tuberculata lamellosa***

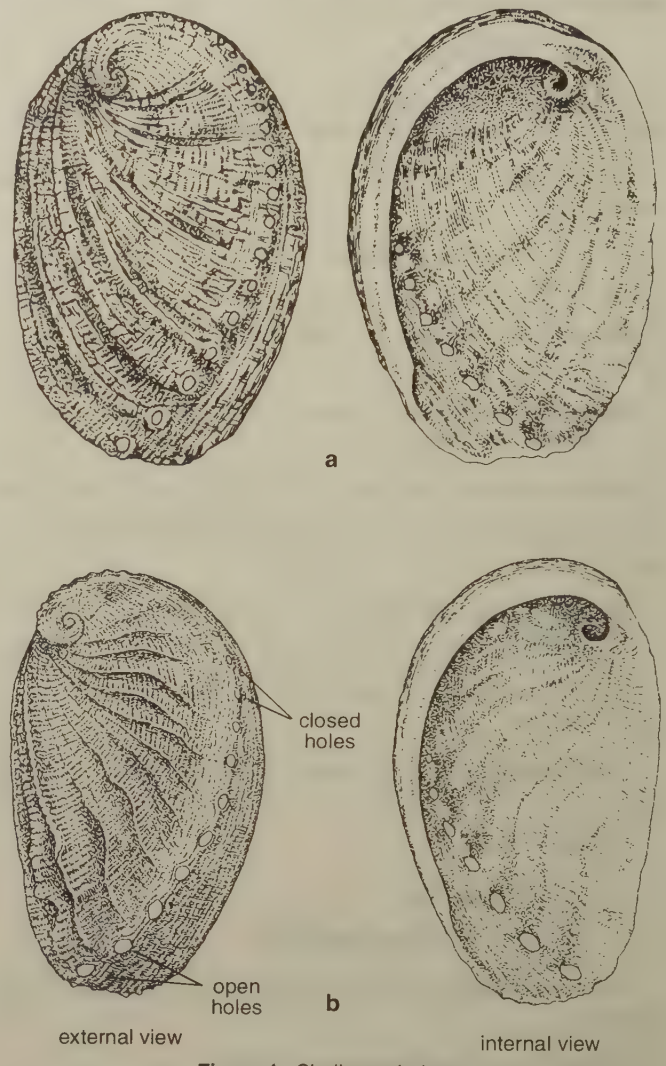

Figure 1. Shell morphology

a. ***H. tuberculata tuberculata*** **b.** ***H. tuberculata lamellosa***

H. t. lamellosa is present throughout the Mediterranean Sea: in the eastern Mediterranean, it occurs in Egypt, Israel, Lebanon, Syria, Cyprus and the Aegean Sea; in the western Mediterranean, it lives in the Adriatic Sea, the Western Basin (northern and central areas, North Africa) and Alboran Sea (Barash and Danin, 1992). Specimens with a ***lamellosa*** shape have been recorded in the Atlantic, especially from northern Spain (Poppe and Goto, 1991).

1.2.4 Standard common names, vernacular names

The accepted English common name for ***Haliotis tuberculata*** in Europe is ormer which is a contraction of the French words "oreille de mer". However, it is known by various common names in several European countries.

The list of common names presented below follows Ebert (1969), OECD (1978), Riedl (1983) and Poutiers (1993).

Ormer, Omar, Venus ear, Sea ear, Ear shell	English
Norman shell, Mother of pearl	Old English
Oreille de mer, Ormeau, Si-ieu, Haliotidae, Silieux, Oreille de Saint Pierre, Ormet, Ormier, Six-yeux	French
Ohrschnecke, Meerohr, Seeohr	German
Lapa Burra, Orelhas	Portuguese
Señorina, Oreja de mar, Peneira, Criba	Spanish
Orecchiale, Orecchia marina, Orecchia di San Pietro	Italian
Patella Reale	Italian (Sicily)
Haliotis, Achivada chromasisti, Aftí tis Afroditi	Greek
Petrovo uho, Uhomorsk, Puzlatka	Yugoslavian
Havsöra	Swedish
Zee-oor	Dutch (Flemish)
Søøre	Danish
Saeeya	Icelandic
Deniz kulagi	Turkish
Orella de mar, Sebateta de la Mare de Déu	Spanish (Cat)
Ozemyam	Hebrew

1.3 Morphology

1.3.1 External morphology

Ormers grow up to 123 mm in shell length (Stephenson, 1924). The most conspicuous feature of the ormer and other abalone species is the ear-shaped shell that covers and protects the soft body parts (**Figure 1**; see Section 1.2.1.3). The colour of the shell is grey to red, according to the type of rock in the surroundings (Crofts, 1929) and the algal diet. As is common in snails, the ormer shell is in the form of a spiral, but the spire is relatively tiny and contains only a minute coil of the visceral mass (Crofts, 1929). The shell is shallow, only about a fifth as high as it is long (Fallu, 1991). Most of the shell is one unusually large body whorl which creates an enormous aperture, thus permitting the shell to cover and protect the foot even when it is fully extended. The whorl is marked externally by many narrow, slightly wavy spiral ridges of varying breadth, separated by narrow grooves, and many microscopic growth lines. At irregular intervals, these are raised into wave-like crests, marking probably pauses in growth (Fretter and Graham, 1976). The most obvious feature on the ventral side of the animal is the large muscular foot which fills the shell opening. The dorsal part of the foot is surrounded laterally with a collar called the epipodium, which is studded with small sensory organs and tentacles (**Figure 2**). Anterior to the foot is the head, which is typically snail-like with tentacles similar to those on the lips, but larger. The mouth is at the base of the head underneath the lips. The mouth contains a toothed radula (for rasping food). Between the shell and the foot in the posterior half of the animal is the gonad which envelopes the digestive gland (liver) and together they form a large cone-shaped appendage, sometimes called the conical

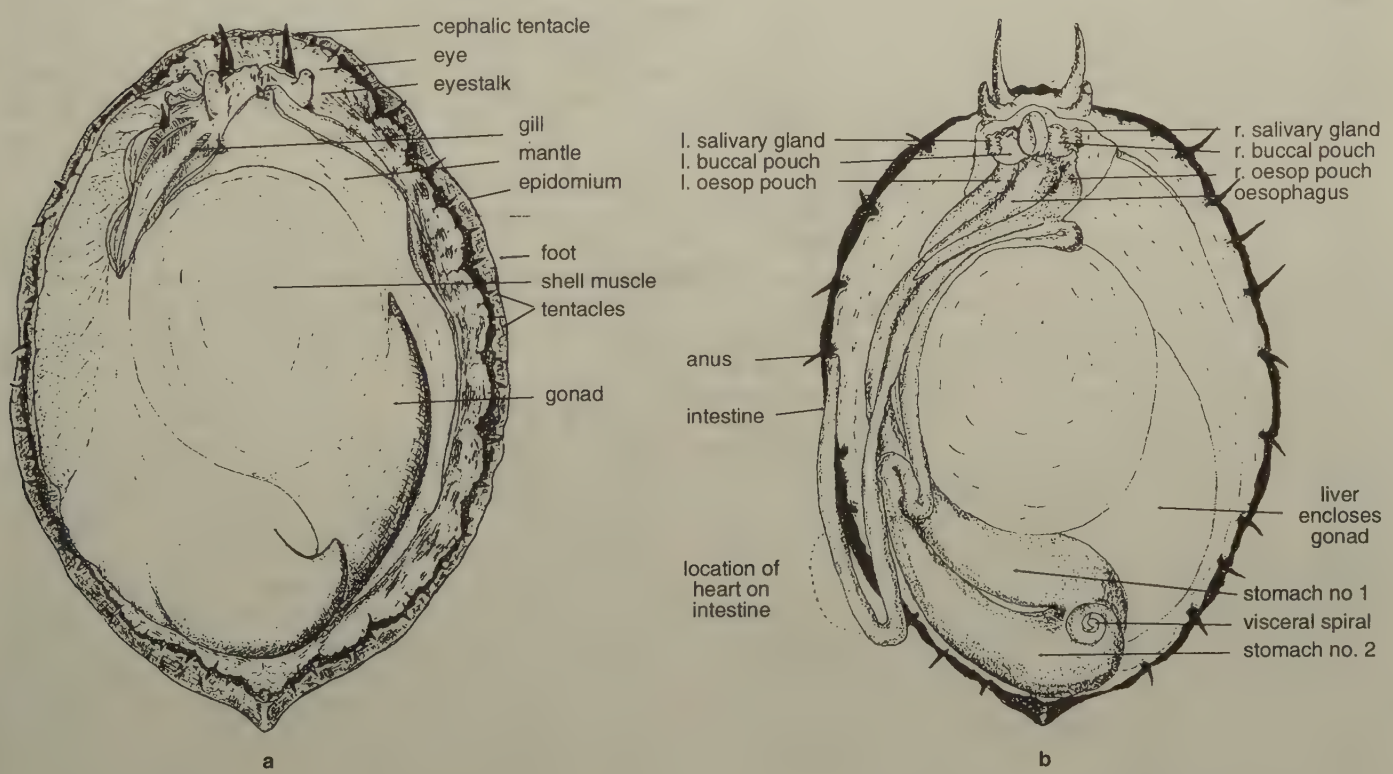

Figure 2. a. Dorsal view of ***Haliotis*** with shell removed and mantle cavity exposed; **b.** The ***Haliotis*** alimentary tract, ctenidia and viscera removed. Dotted lines show the position of the heart (after Cox, 1962).

appendage (Mottet, 1978). The animal is brownish or greenish with a speckling of darker colour, green or white. The darker colour is usually concentrated in areas between the papillae of the foot, epipodium and lips, on the snout and extremeties of the body. Bands of dark and light colour often alternate on the epipodium, giving a striped appearance. The tentacles are usually green and the sole of the foot is often pinkish (Fretter and Graham, 1976).

1.3.2 Cytomorphology

In a karyological study to determine the number and morphology of the chromosomes of ***H. tuberculata*** Colombera and Tagliaferri (1983) and Arai and Wilkins (1986) have shown that the diploid number of chromosomes in this species amount to 28, including 16 metacentrics and 12 submetacentrics.

2. DISTRIBUTION

2.1 Total area

The ormer, ***H. tuberculata*** has a geographic range which extends in the Eastern Atlantic from the Channel Islands and the French coasts of Western Channel in the north (Gaillard, 1958), to the Canary Islands, the Cape Verde Islands, the Azores, the Mediterranean, the North African coast, and the West African coasts of Mauritania and Senegal in the south (Nicklès, 1950; Parenzan, 1970; Nordsieck, 1975). However, it occurs in sizeable densities only off the north of the Armorican peninsula and in the British Channel Islands (**Figure 3**). The species does not occur on the British or Irish mainland, the Channel Isles and Western Normandy, from Chausey Islands to Fermanville near Cherbourg (Hourquet, 1975), mark the northern end of its distribution. The literature on haliotids (e.g. Prince et al., 1987) suggests that these organisms (***H. tuberculata*** included) have a short pelagic larval life with dispersal powers limited by the time available before settlement. Ormers and indeed other haliotids are patchily distributed throughout their range (Forster, 1962; Newman, 1969; Shepherd, 1973) with an affinity for specific habitats (see Section 2.3.5).

2.2 Differential distribution

2.2.1 Spawn, larvae, and juveniles

The eggs produced by ormers are lecithotrophic and considerably heavier than water and if released over a boulder substratum, can be expected to sink and roll down into the substratum before hatching. Lodgement of the eggs within the substratum would prevent them from being rolled across sandy substrata, away from rocky habitat, and would ensure that larvae begin their life in a habitat suitable for settlement (Clavier and Chardy, 1989). The trochophore larvae hatch and swim actively as part of the plankton. The planktonic phase of abalone species is generally short (Mottet, 1978) and in ormer is reported to be 4 to 5 days (Koike, 1978). Further development gives rise to veliger larvae, which at some stage become competent to settle, which cease swimming and enter the benthic phase (Koike, 1978; Mottet, 1978).

Figure 3. Distribution of ***Haliotis tuberculata*** (+) and ***Haliotis lamellosa*** (*).

Larval settlement is known to be attracted by physical, chemical or biochemical cues associated with the adult abalone, leading to an extremely restricted dispersal of larvae (Underwood, 1979; Prince et al., 1987). Forster et al. (1982) speculated that in cool summer waters (16-18°C), the planktonic period for ormer larvae could be prolonged to 5 or 6 days, during which time South West winds could transport larvae from Brittany to reseed ormer beds in the Channel Islands. Juveniles are found attached to a variety of substrates characterized by crustose red algae in the intertidal rocky habitats, usually in shallow water down to 8 metres below chart datum (Clavier and Chardy, 1989; Clavier and Richard, 1986a).

2.2.2 Adults

Adult ormers occur in the same habitat as juveniles. This coexistence may be attributable to the lack of real migration; an adult individual moves up to a few hundred metres from its settlement area (Clavier and Chardy, 1989). They are capable of crossing sand (Werner, 1993) or gravel, but usually require a firm substrate.

2.3 Determinants of distribution changes

2.3.1 Temperature

The distribution of ormer is obviously affected by temperature. Natural temperatures in the Channel Isles range from *ca.* 8°C in winter to *ca.* 17°C in the summer (Hayashi, 1980a). Further south, near ormer populations summer temperatures can exceed 20°C. Forster et al. (1982) presented data which suggested that the decline in the ormer populations of the Channel Islands during the 1960s, and previous shortages in the 1920s and 1890s appear to be related to periods of below average temperatures, particularly during the summer months. Larval period is also affected by temperature. Koike (1978), for example, found that the period from spawning to settlement was 3.5 to 5 days at 20°C and Hayashi (1980a) found it took 60-70 hours at 17.2-19.2°C. With sea temperatures of 16-18°C larval life would be prolonged, as in cooler summers (Forster et al., 1982).

According to Peck (1989) temperatures between 8.5 and 9.0°C approximate the long-term lower lethal limit for ***H. tuberculata***. At the lower temperature ormers are severely limited in their ability to absorb food and grow (Peck, 1989). Laboratory studies have shown the maximum scope for growth for ormers to be at 20°C (Emberton, 1982; Peck, 1989).

2.3.2 Salinity

Ormers generally occur in areas of oceanic salinities. Fretter and Graham (1962) state that ***H. tuberculata*** can not readily tolerate brackish conditions. Beudant (1816), quoted by Jeffreys (1865) and Stephenson (1924), showed ***H. tuberculata*** to be unusually vulnerable to lowered salinity. Laboratory studies (e.g. Peck, 1983) have demonstrated that ormers can survive short term immersions in salinities down to 14‰ and could sustain some growth in salinities down to 24‰.

2.3.3 Currents and wave surge

Juveniles are found preferentially in places that are sheltered from the main tidal currents (Clavier and Chardy, 1989). As they grow and become large, individuals may be found in less sheltered places (Clavier and Chardy, 1989).

Wave surge is an irregular event, but may have an influence on the range of movement of individuals when the habitat is disturbed (Poore, 1972), or when individuals have been knocked loose from the substrate (Minchin, 1975). Wave surge may also induce natural mortality, as individuals are crushed by rocks during storms (Mottet, 1978).

2.3.4 Food

Distribution of ***H. tuberculata*** is largely independent of the surrounding algal community (Clavier and Chardy, 1989). However, ormer habitat is closely tied to a regular supply of drifting algae carried by currents. The quantity of such drift algae determines ormer density where habitat is suitable (Clavier and Chardy, 1989).

2.3.5 Habitat

Ormers prefer shallow sublittoral rocky habitats that contain fissures and crevices in bedrock (Forster, 1962; Forster et al., 1982). They also like rock ledges and the underside of boulders lying on bedrock or sand (Stephenson, 1924; Forster, 1962). Such habitats provide a firm substratum, allowing for an optimal adherence of the foot to resist predators and is firm enough to avoid dislodgement by waves and surge (Crofts, 1929). It also offers shade from direct illumination (Crofts, 1929) and shelter from predators. Abundance and biomass of ormers have been shown to increase with increasing complexity of the habitat (Clavier and Chardy, 1989). Pink crustose algae (mainly ***Lithothamnium*** spp.) are generally considered to offer an optimum substratum for larval settlement at metamorphosis (Morse and Morse, 1984). Forster (1962) observed high densities of adults on rock surfaces encrusted with pink algae.

2.3.6 Behavioural adaptation

Circumstantial evidence suggests that abalone have behavioural adaptations which aid in restricting population distribution through larval dispersal (Prince et al., 1987). Spawning and settlement of larvae occur during the period of calm conditions (Clavier and Chardy, 1989). These observations suggest that ormer populations possibly select conditions of low water movement for spawning, adaptive behaviour which would minimize dispersion of gametes and larvae. Hayashi (1980a) noted that spawning of ormer populations in their natural environment occurs over a short period around August-September when the water temperature is near its maximum and possibly coinciding with brief localized conditions of low water movement.

2.4 Hybridization

No hybrids of ormer are known.

3. BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

Ormers are gonochoristic, though rare cases of mosaic hermaphroditic animals have been reported (Girard, 1972; Cochard, 1980). Sexing of mature ormers can generally be done by visual inspection if the foot and mantle are forced away from the right side of the shell to expose the horn-shaped conical appendage (Stephenson, 1924). Male gonads may be cream or cream with a greenish tinge, while female gonads are usually dark green with various shades of grey-green (Stephenson, 1924; Crofts, 1929). However, spent ovaries may be cream coloured like the male gonads, and it may not be possible to distinguish the sexes (Stephenson, 1924; Forster, 1962). There is no sexual dimorphism of shell structure. There are no significant differences in shell morphometrics of male and female ormer (Y.D. Mgaya, unpublished data).

The mechanism of sex determination in ormer was studied by Cochard (1980) who suggested that individuals showed labile gonochorism. According to Cochard (1980) sex determination had a strongly genetic base but may be influenced by environmental conditions.

3.1.2 Maturity

Male ormers mature earlier and at smaller size than females (Girard, 1972; Hayashi, 1980a). In a study at Glénan archipelago, Brittany, Girard (1972) reported that males become sexually mature when 2 years old at 25 to 40 mm in shell length, and females attain sexual maturity at 3 years of age with a size range from 38 to 54 mm. Minimum size of sexual maturity in the Guernsey populations of the ormer was found to be 40 mm and 49 mm for males and females respectively (Hayashi, 1980a). Ormer in Saint-Malo region, France, are not sexually fully mature until they are 4 years old, at 65 mm shell length (Berthou et al., 1985).

3.1.3 Mating

Ormers are broadcast spawners and males and females release their gametes directly into the seawater (Stephenson, 1924; Crofts, 1929).

3.1.4 Fertilization

Fertilization is external, with both eggs and sperm released in synchrony, though males tend to release their sex products first, followed by females (Stephenson, 1924).

3.1.5 Gonads

The gonad is located between the outer epithelial layer of the conical appendage and the digestive gland. Fecundity representing the total number of oocytes in the ovary, increases with size of individual ormers. **Table 1** shows the relationship between shell length and fecundity as determined by several workers. Mottet (1978) proposed that haliotids are highly fecund and have a linear relationship between numbers of mature eggs in the ovary and body weight. Sluczanowski (1986) suggested that the characteristically high fecundity of abalone may have evolved to offset environmental risk.

Table 1. Fecundity estimates of ormer collected from various locations.

Fecundity	Size	Site	Reference
6.2×10^5	80 mm	Brest Bay	Koike (1978)
5.0×10^5	70 mm	Glénan Archipelago	Girard (1972)
5.0×10^5	110 mm	Glénan Archipelago	Girard (1972)
3.8×10^4	49 mm	Guernsey	Hayashi (1980a)
5.1×10^6	115 mm	Guernsey	Hayashi (1980a)
3.8×10^5	61 mm	Guernsey	Hayashi (1982)
3.4×10^6	101 mm	Guernsey	Hayashi (1982)
4.0×10^5	20 g	St. Malo	Clavier (1992a)
3.8×10^6	160 g	St. Malo	Clavier (1992a)

The most reliable methods for determining reproductive state are gonad index and oocyte size frequencies (Hahn, 1989a). The widely used gonad index convention is described and illustrated by Hayashi (1980a). The sectioned conical portion of the visceral mass reveals the gonad sheathed in digestive gland. The relative proportions of these visceral mass components indicate degree of gonad ripeness:

Gonad index = (gonad area/total area of cross- section) x 100

Tutschulte and Connell (1981) reported a modified gonad gulk index which gives a sensitive estimate of the change in gonad volume:

Gonad bulk index = estimate of gonad volume / body weight.

3.1.6 Spawning

Spawning time varies from island to island in the Channel Isles. Stephenson (1924) and Hayashi (1980a) indicated that spawning in ***H. tuberculata*** populations is not synchronous, but occurs over a relatively short period in late summer (August to September). Using volumetric index of the gonad maturity, Girard (1972) showed that a period from mid-June to mid-November is characterized by increased gonad activity in ormer populations near Brittany coast. Crofts (1929, 1937) suggested that the spawning possibly begins in spring and continues into late autumn. Hayashi (1980a) observed Guernsey ormer populations that were only short distances apart spawning at different times. This remarkable reproductive variability within species over relatively small areas, reflects local variability in physical (e.g. water movement) and biological conditions.

Maturation of gametes is influenced by annual temperature fluctuations (Fretter and Graham, 1964), and a strong correlation between gonad development and water temperature has been demonstrated (Girard, 1972; Hayashi, 1980a). Cochard (1980) showed that differentiation and maturation of the gonad depend on seasonal variations in the photoperiod. Hayashi (1980a) suggested three factors which act in concert to trigger spawning in ormer populations:

(a) the degree of maturation,

(b) the intensity of stimuli, and

(c) the conditions to which ormers are exposed when stimuli occur.

Other factors influencing abalone spawning are: presence of gametes of conspecifics in ambient water, neural or hormonal factors, and availability of food (Shepherd and Laws, 1974; Morse et al., 1977; Mottet, 1978).

After spawning, the gonads become very soft and filled with a gelatinous substance, and some gonads are hollow inside (Girard, 1972; Hayashi, 1980a). According to Hayashi (1980a) the ovary contains very few developing primary oocytes and resorption of ova occurs from December to February. Oocytes develop slowly from February to April, and then rapidly increase in quantity and size, until maximum density is reached by August (Hayashi, 1980a). Males usually become ripe earlier than females (Girard, 1972; Hayashi, 1980a). The massive foot functions as a nutrient reservoir for spawning (Hayashi, 1983; Section 3.4.3). Hayashi (1980a) hypothesized that spawning seasons in different places appeared to correlate with the latitude. He also noted that in southern parts of the ormer's range, spawning is perhaps twice a year, or for a protracted period if not synchronously, but only once and for a short period near its northern limit (e.g. Guernsey ormer populations).

3.1.7 Spawn

As the eggs mature they increase in size and become rounder in shape (Crofts, 1937). The unfertilized eggs are grey-green in colour. The egg membrane has a thin albuminous layer and a micropyle. The diameter of the egg including the egg membrane is about 180µ (Crofts, 1937). After fertilization, the perivitelline space between the outer layer and egg membrane increases in size (Crofts, 1937). The fertilized eggs have a diameter of 210µ including the egg membrane; the yolk has a diameter of 170 m (Koike, 1978).

Since gametogenesis is the same in all abalone species studied (Hahn, 1989a), the work of Tomita (1967) on ***Haliotis discus hannai*** Ino which described seven stages in the development of egg is adopted herein for the ormer:

(a) oogonium stage (diameter *ca.* 3-5µ),

(b) chromatin-nucleolus stage (*ca.* 10µ),

(c) yolkless stage (*ca.* 50µ),

(d) oil drop stage (oil drops measure about 7µ , eggs measure *ca.* 50-90µ),

(e) primary yolk globule stage (*ca.* 150µ),

(f) secondary yolk globule stage (*ca.* 150-180µ),

(g) mature stage (egg measures *ca.* 150-200µ).

Mature eggs have numerous yolk and lipid granules in the cytoplasm, and pigment granules in the cortical layer prior to spawning (Crofts, 1929). The eggs escape via the cavity of the definitive right renal organ through the shell perforations (Mottet, 1978). The eggs are puffed upwards and sink due to having a higher density than sea water (Stephenson, 1924; Crofts, 1937).

3.2 Pre-adult phase

The pre-adult phase has been adequately described by Crofts (1937) and Koike (1978), and the main events are summarized herein.

3.2.1 Embryonic phase

The development of ormer eggs in the laboratory was described by Koike (1978). He reported that with 20± 1°C, the first polar body appears a few minutes after fertilization, followed by the second polar body (**Figure 4a**), but often this is not observed.

First cleavage: Cell cleavage is total, unequal and spiral. The first cleavage is along the vertical axis of the egg, 1 hour 20 minutes to 1 hour 50 minutes after fertilization (**Figure 5b**).

Second cleavage: Occurs along the same axis as the first division 1 hour 40 minutes to 2 hours 10 minutes after fertilization (**Figure 4c**).

Third cleavage: Occurs just above the horizontal axis of the egg after 2 hours 20 minutes, and at this stage micromeres and macromeres are clearly differentiated. The micromeres move around the macromeres in clockwise direction (**Figure 4d**).

Fourth cleavage: This takes place after 3 hours 15 minutes, and the direction of division is counterclockwise (**Figure 4e**).

Morula stage: The embryo reaches this stage after 5 hours (**Figure 4f**).

Gastrula stage: After passing through the blastula stage, the gastrula stage is reached after 8 hours 30 minutes to 9 hours.

Trochophore stage: After 10 hours, cilia appear at the trochophore stage, and they cause the embryo to rotate intermittently inside the egg membrane (**Figure 4g**). The embryo is classified as a trochophore larva when the stomodeum is formed and cilia along the prototrochal girdle are completely formed (Boutan, 1899; Fretter and Graham, 1962).

3.2.2 Larval and early juvenile phase

The following descriptions were taken from Crofts (1937, 1955) and Koike (1978).

Pelagic phase:

Day 1. The larvae begin moving more frequently inside their egg membranes, which become thinner, and finally burst. Apical cilia aid the larvae in bursting the egg membranes during hatch out. After 13 hours, trochophore larvae free themselves from their egg membranes, and immediately swim to the water surface using their preoral ciliated ring or prototroch. Such behaviour could aid dispersal of the short-lived larvae. The hatched larvae measure 155µ x 200µ and some larvae have already secreted transparent larval shell from the shell gland. The larvae are positively phototactic. The trochophore larvae continue to develop until they become veliger larvae. Larvae are classified as veligers when the apical region becomes flat and the velum is completely developed and have long cilia, but are no longer phototactic. The early veliger stage, prior to torsion, is reached after 18-20 hours (**Figure 4h**). The larval shell grows from dorsal to ventral, until it covers the body to just below the velum.

Day 2. First 90° torsion of veligers begins at 29-35 hours and takes 3-6 hours to complete. During torsion, the cephalo-pedal mass rotates 90°, followed by the tearing off of the top of the mantle membrane from the top of the

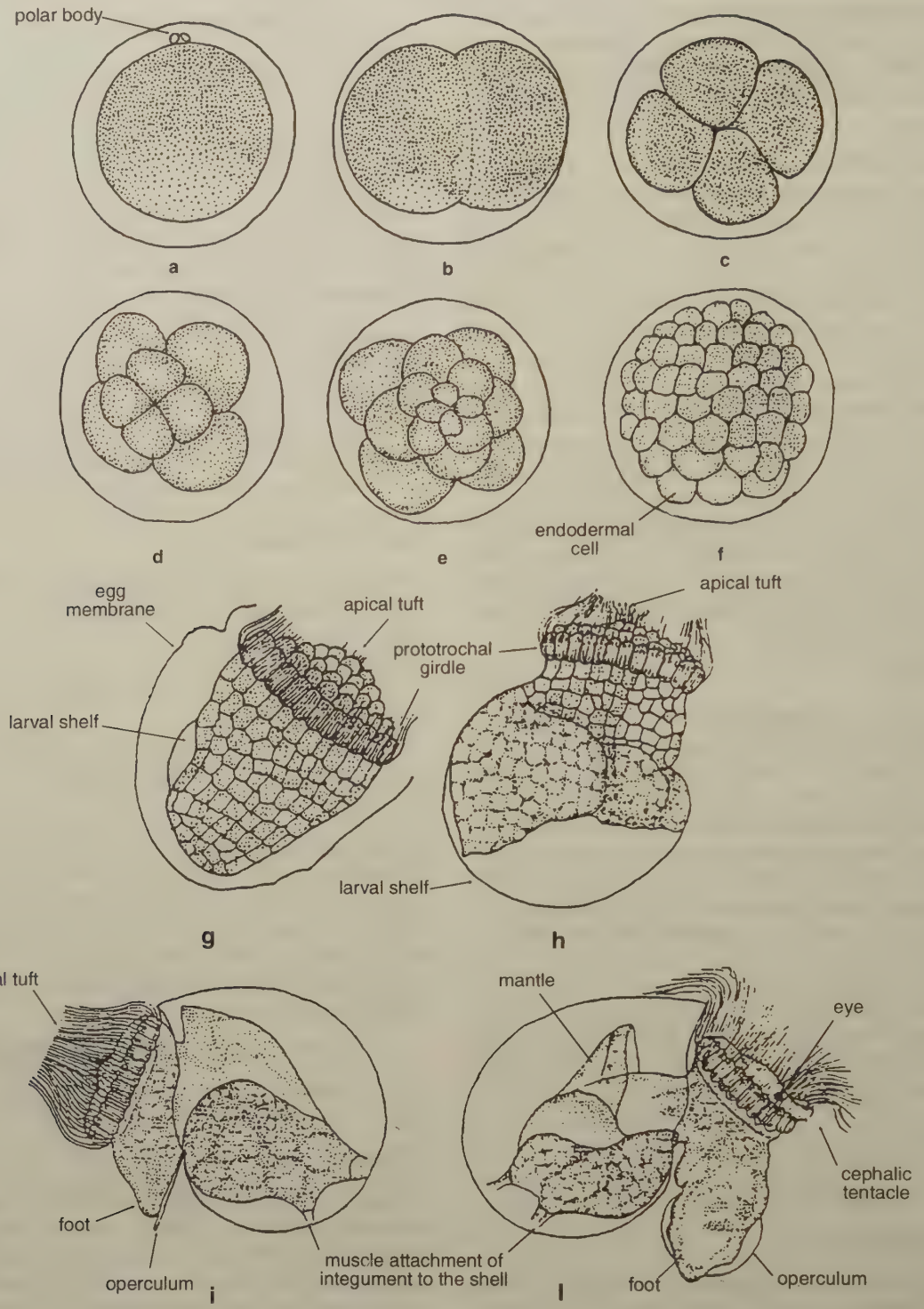

Figure 4. Developmental stages of the ormer showing embryonic and planktonic larval phase (after Koike, 1978); **a**: Fertilized egg (0.21 mm in diameter). **b**: First cleavage (I hr 10 min-1 hr 50 min). c: Second cleavage (1 hr 50 min). **d**: Third cleavage (animal pole view) (2 hr 20 min). **e**: Fourth cleavage (3 hr 50 min). **f**: Morula (4 hr 50 min). **g**: Trochophore just before hatching (13 hr; 0.15 x 0.20 mm). **h**: Early veliger larva (20 hr 20 min; 0.20 mm in diameter). **i**: Veliger larva after torsion (38 hr 30 min - 40 hr). **j**: Veliger larva in late planktonic stage (4.5 days; 0.26 mm in shell diameter).

larval shell. The velum and cephalo-pedal mass rotate between the region of the body covered by the larval shell and the "waist." The region destined to become the mouth and the foot continues to rotate, until the cephalo-pedal mass is rotated 180° from the original position (see second torsion event below). The foot and operculum develop (**Figure 4 i**). Larvae are capable of retracting themselves into their shell, indicating the development of the velar retractor muscle. The velum separates into two parts and rudiments of cephalic tentacles and eyes appear at the centre of each part. The larval shell is 0.26 mm long. The veligers swim in rotating fashion. Cephalic tentacles with papillae develop gradually, and the rudiments of epipodial tentacles appear on both sides of the foot.

Transition from pelagic to benthic life:

Day 3. By the end of the third day, cilia start to develop on the pedal sole and the first signs of settlement behaviour are observed (**Figure 4j**). Many of the larvae can change the shape of their foot and attach it to an available surface, but do not stop swimming unless suitable settlement substratum is present. The non-feeding (lecithotrophic) larvae utilize stored yolk reserves until metamorphosis.

Benthic phase:

Days 4-5. After about four to five days the benthic veliger stage is established, and larvae can be seen creeping around, making exploratory movements characteristic of settling larvae. In each benthic veliger the papillae of the cephalic tentacles have become more numerous; the velum has diminished in size and the snout has begun to protrude at the front of the velum. The statocyst can be observed between the head and foot, with five or six grains grouped together in the centre forming the statolith (**Figure 5a**). Settlement occurs within 3.5 to 5 days after fertilization. Second 90° torsion of the veliger begins about 5 and ends about 12 days after fertilization. Feeding, using a toothed radula to rasp off benthic biota, begins immediately after settlement (Morse and Morse, 1984).

Day 6. Cilia on the velum disappear and the secretion of the peristomal shell begins on the right side of the aperture of the larval shell. The snout is well formed, the

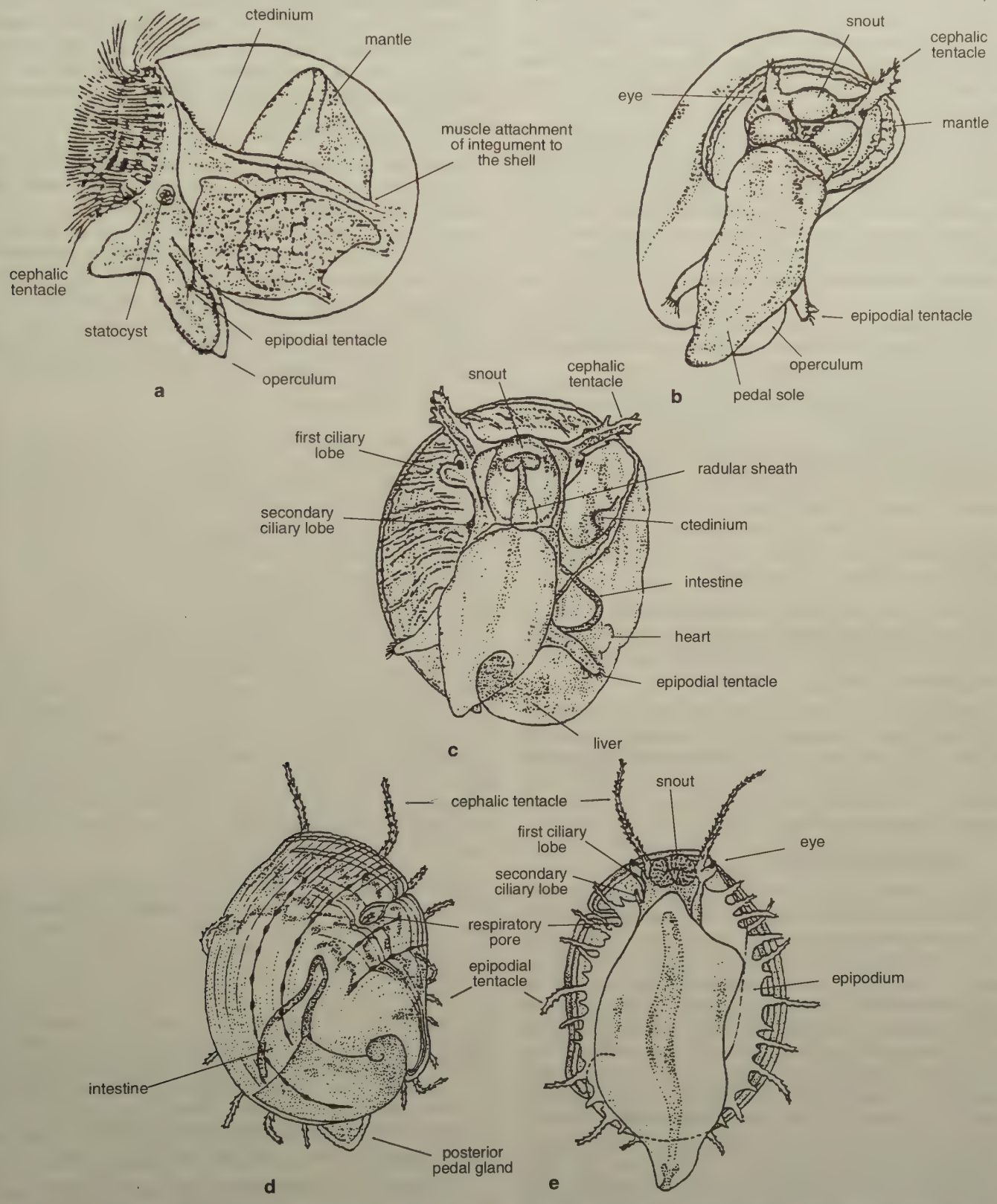

Figure 5. Developmental stages of the ormer showing benthic phase (after Koike, 1978). **a**: Veliger larva in early benthic stage (4.5 days; 0.26 mm in shell diameter). **b**: Creeping larva (ventral view) beginning to secrete peristomal shell (6 days: 0.27 mm in shell diameter). **c**: Creeping larva (ventral view), at the beginning of epipodial differentiation (16 days: 0.47 mm in shell length). **d**: Young ormer with the first respiratory pore (dorsal view) (40 days; 2.2 mm in shell length). **e**: Same as d (ventral view).

pedal sole has become well developed allowing the larvae to creep around actively, and the heart is beating (**Figure 5c**).

Day 9. The spat are 0.37 mm in shell length and have 0.18 mm of new shell growth. The number of papillae on the cephalic tentacles have increased. Movement of the radula is observed for the first time.

Day 12. The final phase of metamorphosis begins and ends about 2 months after fertilization.

Day 16. The spat measure 0.47 mm in shell length and have become flat in shape with the gradual growth of the peristomal shell covering the right side of the body. The first development of the left ctenidium can be recognized in the branchial chamber (**Figure 5c**).

Day 25. The spat have shell dimensions of 0.98 mm and 0.89 mm for length and breadth respectively and the shell shape has become almost circular. Brown patterns appear in the patches on the surface of the shell. The cephalic tentacles become longer and have more numerous papillae. The epipodial tentacles develop in four pairs and the dark line of the intestine can be seen through the shell. The left ctenidium in the branchial chamber is developed and more branched. Feeding behaviour is very active at this stage, and the areas of grazing on the diatom film can be seen as white patches on the surface of the plastic plates used for settlement.

Day 30. A cleft in the margin of the shell on the right side of the head forms.

Days 38-40. The cleft formed earlier becomes a hole in the shell thus marking the formation of the first respiratory pore. The spat measure 2.0-2.2 mm in shell length. The visceral hump can be seen as a violet patch through the shell. At this time 14 or 15 pairs of epipodial tentacles are present (**Figure 5d,e**).

Day 50. The spat reach a shell length of 2.5-2.6 mm in shell length and the epipodial tentacles number 20-22 pairs. The second respiratory pore develop and the inside of the shell is nacreous.

Days 85-90. The spat reach a size of 3.1-3.3 mm in shell length and there are 26-27 pairs of epipodial tentacles. Four respiratory pores were formed but the first one is already closed. At this time many spat were observed feeding on the green seaweed, ***Ulva*** spp. growing on the plates.

3.2.3 Juvenile phase

Koike (1978) observed that at about 160 days after fertilization, the spat reach a size of 6.2 mm in shell length and the number of respiratory pores increases to 9-10 of which 4 or 5 pores are open. The cephalic tentacles grow to about the same length as the shell and the epipodial tentacles become more numerous. The number of respiratory pores continues to increase with shell growth but close gradually except for the functional 3-6 pores nearest the front margin of the shell. The colour of the shell changes depending on the different seaweed on which they fed. Koike (1978) notes that the colour of the shell is reddish brown when the spat have been feeding on diatoms, green when feeding on ***Ulva*** spp. and ***Laminaria*** spp., and changes to red when feeding on ***Palmaria palmata***. By the 435th day after fertilization, the juveniles reach an average size of 21.15± 3.87mm in shell length with a shell breadth of 12.77± 2.25 mm (Koike, 1978).

3.3 Adult phase

3.3.1 Longevity

Ormers grow up to 12.3 cm in length (Stephenson, 1924), and are known to live at least 12 years and may reach an age of 15 years or more (Berthou et al., 1985).

3.3.2 Hardiness

Ormers are relatively well adapted to their natural environment and are capable of utilizing a variety of rocky habitats and food sources (Crofts, 1929; Forster, 1962; Clavier and Chardy, 1989). They also adapt well to captivity and can be maintained for long periods (B. La Touche, South West Aquaculture, Bere Island, Cork, pers. comm.).

3.3.3 Competitors

Competition between ormer and other species has not been examined experimentally, so any account of competition is speculative. There are few studies regarding the competitors of ormers. In the Saint-Malo region Clavier and Chardy (1989) noted that competition from other grazers was not a problem for ormers and therefore could not be an important factor in their survival. However, they pointed out that given a suitable habitat, intraspecific competition for limiting resources (space and food) could set the upper limit for ormer populations.

3.3.4 Predators

The main predators of ormers are ***Octopus*** spp. (Stephenson, 1924; Crofts, 1929) and starfishes (***Asterias rubens, Marthasterias glacialis***) (Stephenson, 1924; Crofts, 1929; Forster, 1962). Starfishes are generalist predators that capture emergent ormers or scavenge stressed or moribund animals (Shepherd and Breen, 1992). Octopuses are known to attack their prey either by drilling a characteristic hole in order to inject poison (Ambrose and Nelson, 1983), or may physically pull the individual off the substratum. Numerous mesogastropods have been reported as predators but attack only aged, weakened or stressed animals by inserting the proboscis into the soft tissue. The genera involved are ***Nassarius*** and ***Buccinum*** (Clavier, 1982; Clavier and Richard, 1985). Crabs, notably ***Necora puber*** and ***Carcinus*** sp. are important predators of young ormers but not adults (Clavier and Richard, 1985). Crab predation is often recognizable because the ormer shells are chipped at the margin (Clavier and Richard, 1985).

The fish predators recorded are mostly wrasses, notably ***Labrus bergylta, Symphodus (Crenilabrus) melops*** and ***Blennius*** sp. Like crabs, they may select the size of prey according to their ability to remove them (Clavier and Richard, 1985). Large fish, rays and small sharks (dogfish) attack ormers by various modes: ramming and fracturing the shell, crushing the shell with the teeth or prising the animal from the substratum (Shepherd and Breen, 1992). The main predatory genera are ***Raja*** (Crofts, 1929), ***Conger*** and ***Scylliorhinus*** (Calvier and Richard, 1985). Shore-birds, notably the oyster-catcher (***Haemotopus*** spp.) and gulls (***Larus***), take ormers from the intertidal zone (Crofts, 1929).

In a study site at the Saint-Malo region, Clavier and Chardy (1989) reported that juvenile density was controlled by natural predation, and that humans were the only threat to adult ormers. However, the cryptic

colouration of juvenile ormers (3 to 20 mm) which inhabit rocky areas covered with the encrusting red algae constitutes an effective defensive strategy against visually searching predators (Crofts, 1929; Clavier and Richard, 1986a).

3.3.5 Parasites, diseases, injuries and abnormalities

Parasites and diseases. There is little information in the literature regarding parasites and diseases of ormers. Crofts (1929) examined over 400 specimens of ormers from the natural population, and two instances of diseased ormers were reported. Inclusive was a female specimen with a severe trematode infection (sporocysts, radiae, and cercariae were present) in the visceral mass, mantle, and ctenidia. The outer surface of the animal was coloured orange from the trematodes. The trematode could not be identified. Also, a male was found with cysts between the gonad and digestive gland. The cysts appeared to be haplosporidian capsules. However, the incidence of infestation appears to be low, and in any event does not appear to affect the health of the animal.

Crofts (1929) also found that ormer shells were frequently bored into by bivalve molluscs such as ***Lithophaga*** *(=* ***Lithodomus****)* sp. and Pholadidea. Clavier (1992b) reported that the red boring sponge ***Cliona celata*** and polychaetes of the genus ***Polydora*** are the major parasites and only shells greater than 50 mm are subjected to infestation. Forster (1967) found the incidence of ***Cliona lobata*** infestation to be acute (up to 95%) in mature ormers. Peck (1983) also found ***P. ciliata*** and ***C. celata*** infestations to be related to animal size. ***Cliona*** and ***Polydora*** species are not parasites in the strict sense of the word, but rather use shells as a shelter. They bore into the shell and in severe cases the whole strength of the shell is lost, which makes the ormer quite vulnerable to attacks from crabs, wrasse and other predators (Forster, 1967) or breakage by rolling stones. Shell infestations do not lead to major physiological stress in the ormers but could cause scraggy muscles thus reducing the meat quality (food value) of infested individuals (Clavier, 1992b). If the shell is penetrated, the individual produces nacre on the inside of the shell, so diverting energy from growth and reproduction (Shepherd and Breen, 1992). Ormer in culture are susceptible to bacterial ***(Vibrio)*** infections (personal observation).

Injuries and abnormalities. Storms may induce injuries when ormers are crushed by rocks and waves (Mottet, 1978). Overturning rocks to locate ormers and the use of metallic objects during fishing may also lead to injuries by crushing and cuts. Knife or bar cut ormers bleed profusely and because ormer blood has no clotting mechanism (Mottet, 1978), the cut individuals may die from loss of vital fluids and their reduced ability to adhere to the substrate, may contribute to mortality from predation and other causes. Similar observations have been reported upon for Californian abalones (Cox, 1962).

3.3.6 Chemical composition

The composition of abalone (raw muscle tissue) was reported by Altman and Dittmer (1968) as follows:

(a) General constituents and energy values (per 100 g edible portion): water 75.8%, ash 1.6 g, fat 0.5 g, carbohydrates (total) 3.4 g, protein 18.7 g, food energy 98 cal.

(b) Minerals: calcium 37 mg, phosphorus 191 mg, iron 2.4 mg.

(c) Vitamins: thiamine 0.18 mg, riboflavin 0.14 mg.

These values should not be treated as constant because the composition of ormer meat, especially carbohydrates varies substantially and is dependent on such factors as the type of diet and reproductive stage and cycle of the animals (Mercer, et al., 1993).

The external shell-layer of ormers have a mixed aragonitic-calcitic composition with the two $CaCO_3$ morphs simultaneously secreted by the mantle epithelium (Dauphin et al., 1989). Kessel (1935) and Mutvei et al. (1985) found that calcite occurs abundantly in the inner part of the external shell-layer (adjacent to the nacre), where it forms large prisms, whereas aragonite occurs in the outer part of that layer as minute irregular radial units.

In a study at two sites on the Channel Island of Guernsey, Bryan et al. (1977) reported concentrations of a number of heavy metals (**Table 2**) measured in the whole soft parts, foot, viscera and individual tissues of ormers.

Table 2. Concentrations of metals in tissues of ***H. tuberculata***. Source: Bryan et al. (1977).

	Concentrations (parts per million dry tissue)				
Metal	**Blood**	**Muscle**	**Gills**	**Left kidney**	**Right kidney**
Ag	0.28	0.35	0.87	6.9	5.5
Cd	0.29	0.24	1.9	4.1	43
Co	0.02	0.12	0.09	4.0	1.1
Cr	0.71	0.38	0.87	n.d	6.4
Cu	560	12.1	103	374	24.2
Fe	47	30.3	436	1021	1200
Mn	3.6	0.49	7.2	5.0	16.6
Ni	0.93	0.29	9.7	27.9	6.8
Pb	1.7	0.68	0.9	6.7	21.1
Zn	19.9	38.0	63.4	124	298
% dry tissue	5.2	28.0	16.9	17.9	25

It was found that with increasing animal size, concentrations of most metals in the edible foot fell, but in the inedible viscera concentrations of cadmium, silver and copper increased. The viscera which accounted for about 26% of the dry weight of soft parts, contained more than 50% of all metals, except nickel, and approximately 90% of cadmium, iron and cobalt (Bryan et al., 1977). Furthermore, highest levels of copper were found in the blood and in the left kidney, whereas high levels of nickel were associated with surface tissues such as the mantle and epidermis of the foot.

3.4 Nutrition and growth

3.4.1 Feeding

Ormers are herbivorous and browse on a variety of seaweeds. Their feeding, as with their movement, is mainly nocturnal (Crofts, 1929; Mottet, 1978). Ormers are relatively inactive (Hayashi, 1982) and do not forage unless they are unable to catch sufficient drift algae. Mottet (1978) reports that they adopt a distinctive feeding

posture when waiting to catch drifting seaweeds. This involves elevating the shell, extending the tentacles, and elevating the anterior part of the foot (personal observation). The captured seaweed is pulled under the shell by the foot where it may be promptly eaten, or held to be consumed later (Mottet, 1978). This behaviour has been observed at night in the hatchery at the Shellfish Research Laboratory at Carna (I. Werner, pers. comm.). The food is rasped off with a powerful radula which is of rhipidoglossate type (**Figure 6**). Young ormer feed by rasping the substrate with their radula for benthic diatoms and coralline algae with bacterial epibiota.

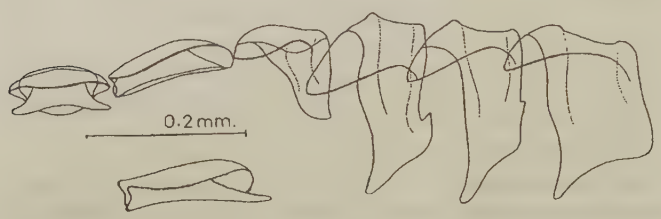

Figure 6. ***Haliotis tuberculata*** radular teeth, showing (from left) a central tooth and five lateral teeth (after Gaillard, 1958).

Feeding appears to decrease with lowered temperatures. Peck (1989) observed that food ingestion declined rapidly and juvenile ormers ceased feeding at temperatures between 8.5 and 9.0°C. Also, ormers may cease feeding during spawning (personal observation).

3.4.2 Food

The food of juvenile ormer is the encrusting coralline algae and its associated epibiota found in their nursery habitat. As they grow, juvenile ormer assume the adults' herbivory, showing a preference for delicate algae and in particular red algae such as ***Palmaria palmata*** (previously known as ***Rhodymenia palmata;*** Guiry 1974) (Koike et al., 1979; Mercer et al., 1993), ***Delesseria*** and ***Griffithsia*** (Bossy and Culley, 1976), but will eat other coarser seaweeds such as ***Laminaria*** spp., ***Ulva lactuca, Chondrus crispus, Enteromorpha intestinalis*** (Koike et al. 1979; Culley and Peck, 1981). Jeffreys (1865) first reported the occurrence of different species of diatoms and of spicules of sponges in the stomach of ormers; Tanner (1926) considers that ormers which live under stones feed on the fine growths *in situ,* usually branched bryozoa, or hydroids, and rarely made up of algae.

Ormers may consume up to 39% of their weight in seaweed per day, but with the better food values, 10-20% seems more typical (Mottet, 1978). Young ormers are known to eat other things besides macroalgae; for example, small juveniles, less than a year old, usually depend on a diet of benthic diatoms and coralline algae (Crofts, 1929). In the laboratory spat have been observed to graze along the bottom of rearing containers and may leave distinctive feeding tracks (Koike, 1978).

3.4.3 Growth rate

Ormers grow at a slow rate, and it takes a minimum of 3 years for ormers to grow to a moderate size of 45 mm in shell length (Forster, 1967; Clavier and Richard, 1986a). Growth is most often measured by the conventional shell dimensions illustrated in **Figure 7**. Shell length is the usual measurement used to indicate the size of ormers, and it tends to be a better indicator of age than weight because it varies much less seasonally (Mottet, 1978). However, length measurements become less useful in older animals because there may be little or no increase in shell length, and sometimes edges of the shell erode faster than new material can be added (Mottet, 1978). Several workers have studied growth of ormer populations in the wild (Forster, 1967; Hayashi, 1980b; Cochard, 1982; Clavier and Richard, 1985, 1986a) and in the laboratory (Koike et al., 1979; Peck, 1989). Hayashi (1980b) used annual rings in estimating age and growth in ormer. Both Forster (1967) and Hayashi (1980b) used shifts in shell size-frequency modes and assessments of growth rates to verify the annual deposition of rings in the ormer.

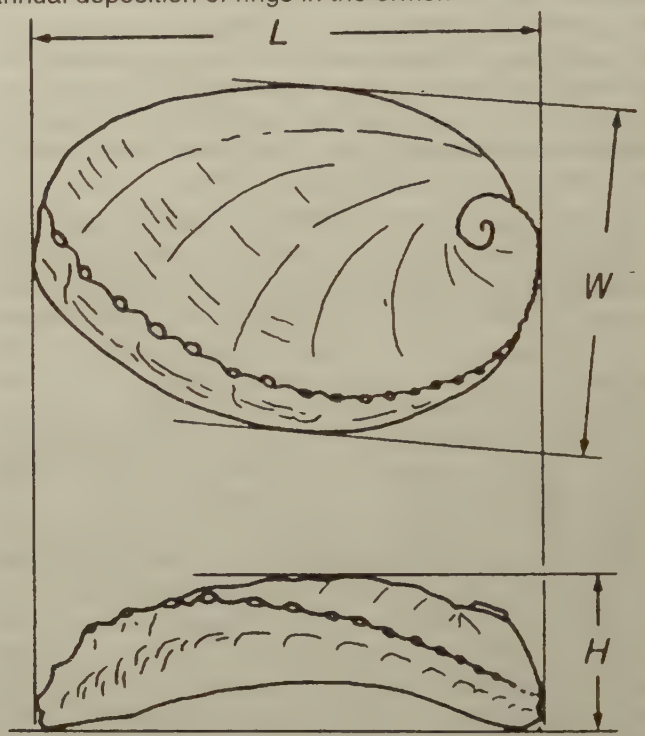

Figure 7 Conventional ***Haliotis tuberculata*** shell measurements of length (L), width (W), and height (H).

Forster (1967) studied the growth of the ormer from Guernsey and found that, to begin with, growth proceeds at a near uniform rate of 15 mm increase in shell length a year. After reaching a length of about 50 mm, at about 3.5 years old, the annual increment declines progressively, until at 100 mm length, although growth continues, increments are negligible. Forster (1967) also investigated the growth rings of ormers and found that the maximum growth for mature adults is between August and December or January, i.e., on cessation of their reproductive activity. This growth accounts for at least 70% of their total annual increment. Forster (1967) thought that the immature ormers probably grow fast all through the summer as they do not participate in reproductive activity. Clavier and Richard (1986a) point out that the rate of growth of the ormer shows a winter reduction, and, on average, about 70% of the annual increase takes place between May and November.

Table 3 summarizes published studies on growth rates in the field for ormer. The parameter t_o of von Bertalanffy growth function has been omitted, as it is often not given or assumed to be zero, and is not very useful in comparing growth rates (Day and Fleming, 1992). The growth of ormer shows considerable variability in space and time. Locality is important to growth because of food supply, exposure to wave energy and local thermal conditions. Season is widely reported to influence abalone growth through changing temperature and algal community conditions. Moreover, growth can be retarded by the diversion of energy into seasonal gonad production (Mottet, 1978; Hayashi, 1983; Clavier and Richard, 1986a). Growth can also vary considerably between different conspecifics kept under the same laboratory conditions (Y.D. Mgaya, unpublished data).

Comparison of Forster's (1967) and Hayashi's (1980b) results reveals that there is a tendency for ormers from an intertidal population to grow faster than those from a sublittoral population (**Table 3**). Hayashi (1977) considered this difference to be attributable to more food being available to intertidal ormers, also wave action enriches the habitat with drift algae. The length-weight relationship for ormer was calculated by Forster (1967) to be: $W = 0.00002009\ L^{3.426}$, W being the weight in grammes and L shell length in millimetres. An examination of length-weight relationship of hatchery-raised ormer revealed no differences between males and females (Y. D. Mgaya, unpublished data). The equations were calculated by using a nonlinear iterative least squares regression with Marquardt's algorithm (Saila et al., 1988):

Male $W = 0.0001006L^{3.105}$ ($n = 205$, $r^2 = 0.96$)

Female $W = 0.0001634L^{2.990}$ ($n = 255$, $r^2 = 0.96$)

Total $W = 0.0001326L^{3.038}$ ($n = 500$, $r^2 = 0.99$)

The amount and quality of meat in ormers with the same shell dimensions will vary depending on seasonal and environmental conditions. Hayashi (1983) reported a drop in condition factor of ormers shortly after spawning. He also found that glycogen is stored in the foot tissue for gonad growth, and changes seasonally in relation to the reproductive cycle, i.e. it decreases as gonad maturation proceeds.

In a study on the influence of population density on growth of juvenile ormers reared in the laboratory, Koike et al. (1979) showed that growth rate decreases with increasing stocking densities. They concluded that, "the

Table 3. Studies of ***H. tuberculata*** growth (adapted from Day and Fleming, 1992).

No. of sites	Method	Model	Parameters	Variation	Reference
2	GMI, T	Linear (<55 mm) VB	15-16 mm/y Subtidal K = 0.39, L_∞ = 99	H S Y	Forster (1967)
	T		K = 0.27, L_∞ =108 Intertidal		
	GMI		K = 0.29, L_∞ = 119		
	GMI				
1	T(CF)	Linear (<55 mm) VB	(Intertidal) >20 mm/y K = 0.45, L_∞ = 115	H	Hayashi (1980b)
1	GMI	VB	K = 0.25, L_∞ =105	H L S	Cochard (1982)
2	CF GMA T	VB	K = 0.37, L_∞ = 108	L Y	Clavier and Richard (1985)
		Gomp	a = 0.53, L_∞ = 105		
1	CF	Inc	35 mm in 2 y		Clavier and Richard (1986a)

Abbreviations: *Method* CF: cohorts from length frequency data followed through time. GMA: length-at-age data from growth checks. GMI: increments in length from growth checks. T: tagging. *Model* Gomp: Gompertz. Inc: growth rate increases with age. VB: von Bertalanffy. *Parameters* a: Gompertz parameter as in Kaufmann (1981). K: Brody growth coefficient in y^{-1}. L_∞ in mm: maximum or asymptotic length. Reported variation in growth H: habitat. L: locality. S: seasons. Y: years.

most suitable rearing density for ormers of 7-10 mm can be considered to be between 2500 m^{-2} - 3750 m^{-2}" (p. 51).

3.4.4 Metabolism

Mottet (1978) observed that the processes by which ingested food is incorporated into abalone tissue and subsequently converted for special functions such as reproduction and mucus production have not been well studied for abalone generally. The quantitative relationship of oxygen consumption of ormers at the hatchery and nursery stages as it relates to body weight, ration, acclimation temperature and ambient oxygen tension has been established (Gaty and Wilson, 1986). They found that ormers exposed to declining oxygen tensions at 16°C showed little ability to regulate oxygen consumption rate. Oxygen dependence was shown to be highest in small starved ormers and lowest in large fed individuals (Gaty and Wilson, 1986). An exponential relation between standard oxygen consumption rate, tissue weight and acclimation temperature following a 14-day acclimation period for ormers was calculated by Gaty and Wilson (1986) to be:

$$VO_2 = 0.06228 \times W^{0.869} \times T^{0.638}$$

where VO_2 is oxygen consumption rate in ml O_2 h^{-1}, W is dry tissue weight in g, and T is temperature in °C. The greater degree of respiratory independence of large ormers, as shown by Gaty and Wilson (1986), would suggest that larger individuals may be more resistant to short-term periods of environmental hypoxia than smaller more oxygen dependent individuals. This observation supports Stephenson (1924) who noted that small ormers (9 mm shell length) are only encountered below extreme low spring tide level, where oxygen levels are stable. It should however, be pointed out that laboratory results, being further removed from the natural environment, may be difficult to interpret in terms of field populations.

Laboratory studies have demonstrated that oxygen consumption in abalone shows a circadian rhythm, with the rate increasing from dusk to mid-night and decreasing from mid-night to mid-day (Hahn, 1989b). This indicates that the most active period and feeding period for ormers are mainly during the initial portion of the dark period.

Ormers, like other organisms, allocate the ingested energy to a variety of pathways in varying proportions and rates. An energy budget equation which takes into account all the animals's activities was developed for ormers by Peck (1983) and Peck et al. (1987). The equation is

$$I = E + G + R + U + M$$

where I = food ingested; E = faeces egested; G = total growth (somatic + reproductive growth); R = respiration; U = ammonium excretion and M = mucus production. They measured each component of the energy budget for the whole size range (0.01-50 g) of ormers held at 15°C, 12 hour light : 12 hour dark photoperiod, and fed ***Ulva lactuca***. The major component of the energy budget was found to be somatic growth (37.5% of I) in a 0.01-g dry wt animal while it was respiration (31.1% of I) in a 50-g dry wt animal. Mucus production formed a large part of the budget, with values ranging from 23.3% of I in a 0.01-g dry wt animal to 29.1% of I in a 50-g dry wt animal (Peck et al., 1987).

Culley and Sherman (1985) showed that an exponential relationship exists between mucus production of ormer and substrate particle size on which the individual is present. In the light of these findings they concluded that smoother substrates will allow energy utilized in areas of the energy budget other than mucus production and may be of some economic importance as far as the commercial culture of the ormer is concerned (see Section 7).

Gäde (1988) described the metabolic characteristics of the shell adductor muscle and the foot muscle of *Haliotis lamellosa* during anoxia and recovery periods. It was found that glycolysis in the shell adductor muscle led mainly to the formation of tauropine, a novel anaerobic end product (Gäde, 1986, 1988). In contrast, D-lactate production predominated in the foot muscle. This pattern was shown to be consistent with the different tasks the two muscles perform, which in turn, lead to different metabolic needs. The shell adductor muscle is metabolically more active than the foot and performs burst contractions which, in general, are dependent on anaerobic metabolism. The foot is mainly responsible for slow gliding movements that very likely are supported by aerobic metabolism. Gäde (1988) further demonstrated that in hypoxic or anoxic conditions, both muscle tissues need to have the capacity for anaerobic metabolism.

3.5 Behaviour

3.5.1 Migrations and local movements

Ormers are known to be mobile animals but generally move slowly (Mottet, 1978). Stephenson (1924) observed ormers travelling at over five metres per minute. During tagging experiments Forster (1967) noted that, most of the 45.3% of the ormers recovered after one year, were taken within the marked off boundary where they had been replaced, after tagging, or within five metres from its border. He also noted that a newly tagged ormer may move three metres in 24 hours and five metres in three days. Clavier and Richard (1984) reported that during one year, 32% of the tagged population did not move and the mean range of movement was 6.7 m for individuals that moved. These observations do suggest that, although capable of moving, ormers do not stray much when settled. The authors also observed that mobility generally decreases with size and age of the animals. Seasonal offshore movement of ormer during the autumn was recorded in Brittany (Clavier and Richard, 1984), probably to avoid storms.

Ormers have a massive, muscular foot (Section 1.3.1) which functions as a complicated hydrostatic system in which a series of muscles contract to generate pressure patterns that cause a range of specific body movements. According to Lissman (1945), movement in the ormer involves longitudinal muscular contraction, followed by relaxation, resulting in waves which pass over the foot in a postero-anterior direction. The author points out that the longitudinally contracted areas are lifted off the ground and move forward, whilst the elongated areas remain stationary. Therefore, during one locomotory cycle any point on the sole will show a phase of forward movement and a phase of rest.

Ormers creep about for a variety of reasons, but most commonly the movements are associated with foraging for food at night (Mottet, 1978). Homing behaviour has been

suspected but there are no data to substantiate its occurrence (Stephenson, 1924; Mottet, 1978). Other reasons for movement include search for a better habitat, for example, young ormers migrate from one type of habitat to another as they grow old (Clavier and Chardy, 1989). Also considerable movement may take place during and after storms when the habitat has been disturbed, or the animals have been knocked loose from the substrate (Clavier and Chardy, 1989). In the latter case, ormers can usually right themselves within a minute by extending the posterior end of the foot by as much as half the length of the shell and moving across the sand until they come in contact with a hard substrate (Minchin, 1975; Werner, 1993).

3.5.2 Schooling

Ormers are benthic and may not conform to the classic schooling phenomenon (i.e. moving around together in unison). Brehant (1958) describes an ormer tagging experiment, using aqualung gear, and concludes that ormers do not move very much, at least in June. Ormers do not increase movement during the spawning season and are not known to form aggregations during the spawning season (Clavier and Richard, 1984; Clavier, 1992a).

3.5.3 Responses to stimuli

Changes in the environment act as stimuli for a change in behaviour or condition of ormer. Some examples of the kinds of environmental changes that often act as spawning triggers are changes in temperature (Hayashi, 1980a), variations in day/night lengths (Cochard, 1980), and the presence of a suitable member of the opposite sex (Croll, 1983). Presence of male sperm in the water would trigger a ripe female to spawn (Stephenson, 1924). Ormer, like other gastropods, possess a precise mechanism for locating foods by chemical cues and also are able to discriminate between foods or potential foods using taste and smell (Croll, 1983). Competent veliger larvae use chemical cues in mucus trails of conspecifics and diatoms to settle and begin metamorphosis (Seki and Kan-no, 1981).

4. POPULATION

4.1 Structure

4.1.1 Sex ratio

Hayashi (1980a) reported a male-to-female ratio of 1:1 (403 males and 383 females) for ormers over 90 mm collected in Guernsey. Crofts (1929) found a preponderance of females for marketable size ormers (39 males and 51 females), but by chi-square test this was found to be consistent with a 1:1 sex ratio (Hayashi, 1980a). Forster (1962) reported a preponderance of males in adult samples in Guernsey. Girard (1972) found a high proportion of females in juvenile ormers and nearly a 1:1 sex ratio in bigger size ormers, and this led him to suggest a possibility of sex change. Bolognari (1953) reported also on gonadal changes in ***Haliotis lamellosa***. Hayashi (1980a) is of the opinion that juvenile ormers tend to first form primary oocytes before becoming mature, hence leading to a possibility of immature individuals being classified as females. Hayashi (1980a) concludes thus, "one should not necessarily conclude that juvenile ormers with primary oocytes in their gonads are females; they could better be described as putative-females" (p. 428).

4.1.2 Age composition

Cochard (1982) examined a sample of ormers from the Bay of Brest, and identified 7 age groups. He showed that age-2 ormers were the most abundant followed by age-1. Age-7 individuals were the least abundant in the population (**Table 4**).

4.1.3 Size composition

Population surveys on ormers in Guernsey (Forster, 1967; Forster et al., 1982) have revealed that between 1965/6 and 1968 few smaller ormers (below 50 mm in length) were found. However, observations in 1973/4 showed a small increase in the frequency of some size groups of smaller individuals (<80 mm) most likely suggesting better recruitment of young ormers to the stock in this case. By 1976 small ormers had again declined to pre-1973 levels. **Figure 8** highlights the change in population of ormers since 1961, namely the failure of recruitment shown by the continued decline in the proportion of smaller ormers, especially between 1961

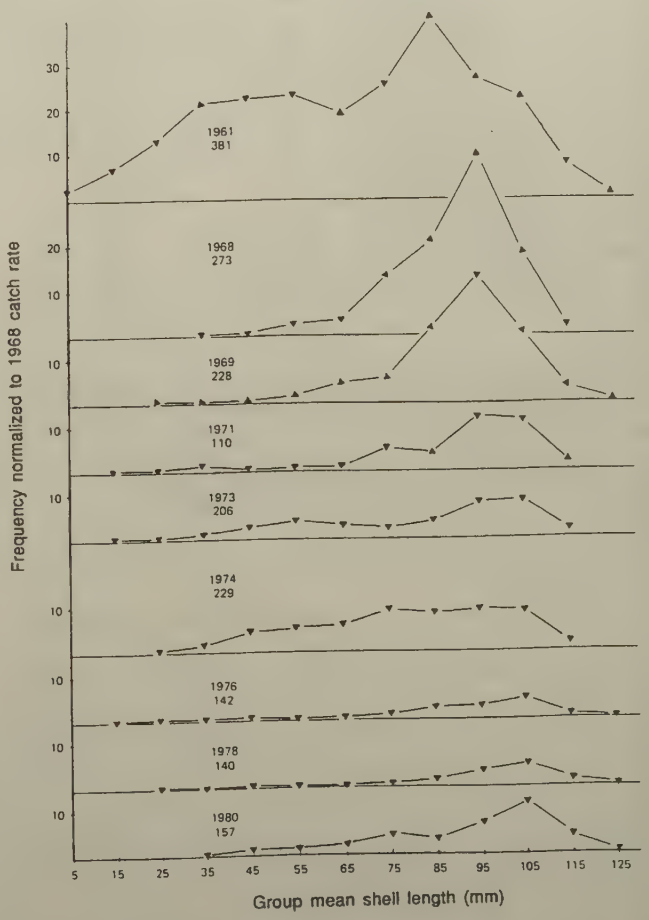

Figure 8. Size frequencies of ormers for south coast of Guernsey. The figure for 1968 represents the normal percentage frequencies, but for later years the figures have been adjusted according to the difference between the mean per 5 min search of every year with that of 1968. The figure for 1961 are based on results from the whole islands scaled up according to the estimated population level in 1961 (after Forster et al. 1982).

Table 4. Growth checkmarks measured and tabulated according to their position on shell (modified from Cochard, 1982).

Position (mm)	Number of individuals at successive annuli						
	1	2	3	4	5	6	7
8	3						
10	14						
12	35						
14	81						
16	117						
18	82						
20	62						
22	28						
24	21						
26	10	2					
28	6	8					
30		18					
32	2	24					
34		42					
36	1	53	1				
38	1	66					
40		81	2				
42		62	4				
44		50	8				
46		25	15				
48		37	28	1			
50		14	50	3			
52		8	57	4			
54		5	75	5			
56		2	55	16			
58			52	13	2		
60		1	39	35	4		
62		3	25	47	3		
64			16	46	7		
66			15	52	12	2	
68			4	39	20	2	
70			4	27	24	6	1
72				29	31	10	
74				18	38	8	1
76				8	27	13	1
78				9	26	16	5
80				3	15	25	6
82				4	8	12	7
84				1	12	10	10
86				1	2	6	14
88					4	15	9
90					2	4	4
92					1	2	2
94					1	1	4
96						1	2
98						1	2

and 1968 (Forster et al., 1982). **Figure 9** highlights samples taken off the west coast of Guernsey. From this figure Forster et al. (1982) point out that in 1961 ormers of less than 80 mm length formed about 60% of the population, which declined to less than 20% by 1969, subsequently the smaller sizes increased in proportion but declined again, so the improvement was not sustained. Forster et al. (1982) concluded that the change in size frequency is possibly related to bad weather and the low temperature of the sea water, especially the exceptionally cold winter of 1963. These two factors according to Hayashi (1980b), could directly or indirectly lead to: (a) the unsuccessful spawning due to poor maturation and perhaps lack of effective stimuli, (b) the mortality of planktonic larvae or settlement failure, or, (c) the heavy mortality of newly settled spat. These suggestions seem plausible as causes of poor recruitment of juveniles.

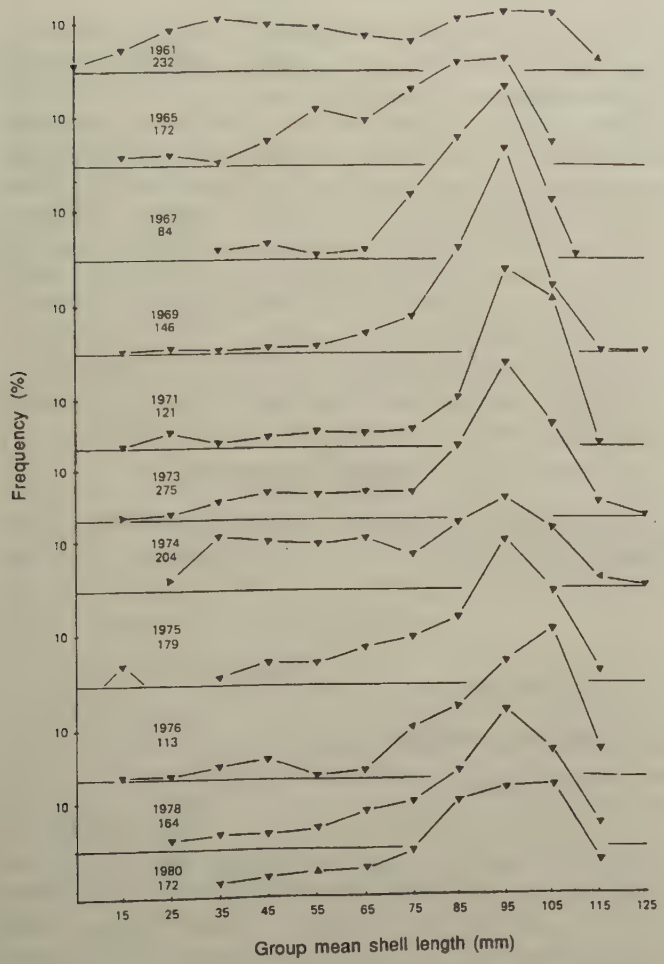

Figure 9. Percentage size frequencies of ormers from the west coast of Guernsey (after Forster et al., 1982).

Peck and Culley (1990) assessed population distributions for 13 sublittoral sites around the coasts of Jersey, Channel Isles using SCUBA techniques. Large animals dominated the overall size distribution such that 68% of the population were over the minimum fishing limit (80 mm shell length; **Figure 10**). In terms of biomass, Peck and Culley (1990) reported that 87% of the standing stock was over 80 mm in length (**Figure 11**). Clavier (1983) and Peck and Culley (1990) found that size of ormers varied with depth at Saint-Malo and Jersey respectively. Large animals were found deeper than small ones, suggesting that ormers settle in shallow water and migrate to deeper localities as they grow older.

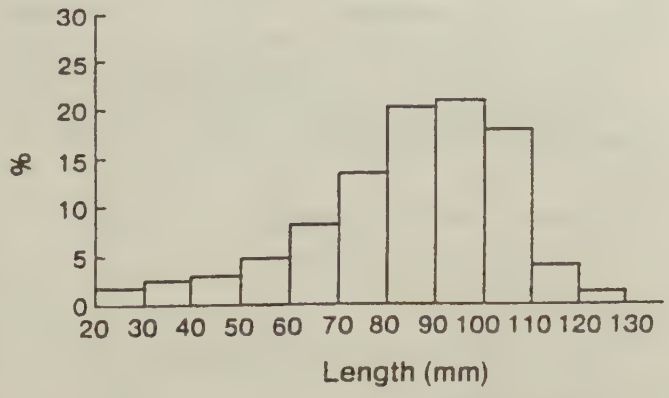

Figure 10. ***Haliotis tuberculata***: the population size distribution for the whole of Jersey, Channel Isles. Data are presented on the basis of numbers of animals in a given 10 mm size range as a percentage of the total number of animals sampled (after Peck and Culley, 1990).

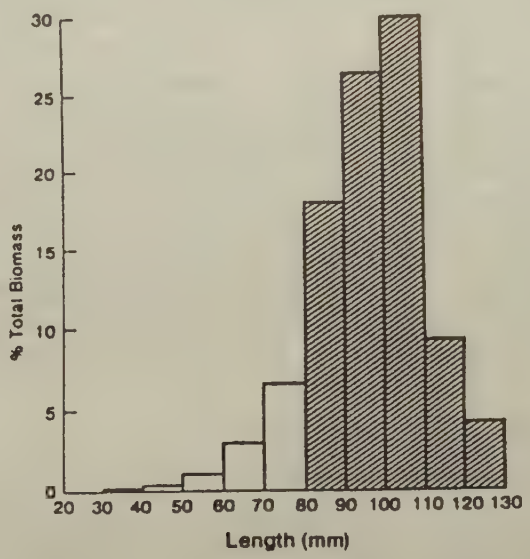

Figure 11. ***Haliotis tuberculata***: distribution of biomass in different length classes for the combined population around Jersey. The shaded area is for animals greater than 80 mm in length, and hence above the present minimum size for collecting. The shaded area represents 87% of the total biomass (after Peck and Culley, 1990).

4.2 Abundance and density

Clavier and Richard (1983, 1986b) reported a mean density of 0.54 animals m^{-2} for Saint Malo. Peck and Culley (1990) found that mean densities range from 0.05 animals m^{-2} to 2.35 animals m^{-2} at 13 sublittoral sites on Jersey, while the overall mean for the whole island was 0.79 animals m^{-2} (s.e.=0.24). Forster (1962) reported a remarkably high density of 2.4 ormers m^{-2} between 0-9 m below low tide at a site in Guernsey. Peck and Culley (1990) examined the correlation between population density and mean animal length of ormers in Jersey. They found that density (D) and mean animal length (SL) were inverseiy correlated. The following equation describes the relationship:

$$\text{Log}_e D = 30.1 - 6.92 \log_e SL \ (r^2 = 0.68;\ n = 13; p<0.01)$$

Clavier and Richard (1983) found that densities of ormers varied with depth at Saint-Malo. Densities tended to be high near the low water level of spring tides and low 5 m below this. Clavier and Chardy (1989) found a strong correlation between densities of juveniles and adult ormers, and attributed this to the absence of real migration.

4.3 Natality and recruitment

4.3.1 Reproduction rates

See Section 3.1.5.

4.3.2 Factors affecting reproduction

See Section 3.1.6

4.3.3 Recruitment

Recruitment is defined here in the fisheries sense as the rate at which abalone become vulnerable to the fishery (Ricker, 1975). The rate of recruitment for ormers is generally considered to be low (Bossy and Culley, 1976; Forster et al., 1982). The overfishing of ormer which is well documented (Stephenson, 1924; Bossy and Culley, 1976), coupled with their apparent susceptibility to "recruitment overfishing" (Gulland, 1973) in which spawning stock is reduced to such a level that inadequate production of recruits ensues appears to be partly responsible for the low recruitment. Poor recruitment of ormers in Guernsey is attributed to low summer temperatures in the 1960s and 1970s (Forster et al., 1982; see Section 4.1.3). Peck and Culley (1990) suggested the density-dependent control of recruitment by adult ormers, whose foraging activity at high densities, smothered recently-settled juveniles.

4.4 Mortality and morbidity

4.4.1 Mortality rates

Berthou et al. (1985) estimated the instantaneous mortality rate for ormer in the Saint-Malo region to be of the order of 0.2 per year based on 5% of a cohort reaching the estimated longevity of 15 years. Haliotids are generally considered to have low instantaneous rates of natural mortality (M) (Shepherd et al., 1982). In unharvested populations, M usually ranges between 0.1 and 0.2 (Shepherd and Breen, 1992) and these populations are characterized by accumulations of larger, older individuals (Hayashi, 1980b; Clavier and Richard, 1985, 1986b; Peck and Culley, 1990). A low value of M is reasonable considering the relatively long life and slow growth of abalone.

Substantial variability of mortality rates occurs related to age, habitat, density and other environmental differences (Shepherd and Breen, 1992). Data presented by Clavier and Richard (1985) show that M decreases with increasing age classes; however, there is evidence that M increases among the oldest (10-12 year) age classes (**Table 5**).

Table 5. Estimated instantaneous rates of natural mortality (M) for ***Haliotis tuberculata***. Source: Clavier and Richard (1985).

M (y-1)*	Age class (years)
1.7	0+
0.26	1-2
0.14	4
0.26	10-12

*Mortality rates were estimated by tag-recapture and population modeling.

4.4.2 Factors causing or affecting mortality

(for predators see Section 3.3.4)

No specific studies have been done regarding factors affecting mortality. Hayashi (1980b) and Forster et al. (1982) suggested that larval ormers had decreased survival in below-average temperatures, resulting in poor settlement in exceptionally cold years. Heavy storms can also cause significant mortalities (Mottet, 1978). Large numbers of animals can be buried by sudden changes in sediment level during storms. High mortality by storms can occur to animals through crushing by dislodged boulders, freshwater runoff, silt and debris (Mottet, 1978; Shepherd and Breen, 1992). Mortality may be induced by some of man's activities. Bossy and Culley (1976) reported that bar cutting, the injury caused to sublegal ormer during fishing and replacement, can also cause serious mortality.

4.4.3 Factors affecting morbidity

(for parasites and diseases see Section 3.3.5; physical factors 3.3.5)

5. EXPLOITATION

5.1 Fishing equipment

5.1.1 Gears

In the Channel Islands ormers are caught with the aid of a strong knife or special "ormering hook" (Bossy and Culley, 1976). This gear is described as a strong metal bar about 30 - 60 cm long ending in a flattened hook which can get between the strong sucking foot of the ormer and the rock to which it clings (Bossy and Culley, 1976). A similar equipment is used by French fishermen on the coasts of Western Normandy and Northen Brittany (Fleury, 1981, 1984). Prior to 1973 divers with SCUBA gear were permitted to catch ormers, but have since been forbidden (Bossy and Culley, 1976; Clavier, 1992c). Thus all ormer fishing grounds are restricted to the intertidal zone where the animals are located by overturning rocks, or by feeling into cracks and crevices with feet or hands (Bossy and Culley, 1976).

5.1.2 Boats

Small boats were used by divers who had one or more assistants to operate the boat and retrieve the ormers (Mottet, 1978). At present, shore gatherers may not need a boat; however, some fishermen in France use a boat when fishing with hook and line for ormers (Berthou et al., 1985).

5.2 Fishing areas

5.2.1 General geographic distribution

(See Section 2.1 and **Figure 2**.)

5.2.2 Geographic ranges

The ormer is mostly caught in the British Channel Isles and in Brittany, France (Clavier, 1992c). As mentioned earlier, ormer gathering is restricted to the intertidal zone up to 8 m below chart datum.

5.2.3 Depth ranges

Density of ormers varies with depth. Clavier and Chardy (1989) showed that a depth below 8 m supports less density, but in the subtidal zone no general relationship exists between density and depth. Further, they pointed out that "maximum depths occupied by ormer are of little importance in the Saint-Malo region but differ along the coast of Brittany and may go beyond 20 m in the western regions" (p. 196).

5.2.4 Conditions of the grounds

Density and biomass of ormers increase with increasing complexity of the habitat (Clavier and Chardy, 1989). Both biotic and abiotic attributes of the habitat are important for ormers. Clavier and Chardy (1989) found that presence of crustose algae and low coverage of large macrophytes supported high ormer densities. Certain types of rocky bottom were found to support high densities, for example, a schistose bottom is preferred to granulitic and sandstone rocks (Clavier and Richard, 1986b; Clavier and Chardy, 1989).

5.3 Fishing seasons

In Jersey Island, ormers are caught from October to April, and in Guernsey from December to April (Bossy and Culley, 1976). Since ormer fishing is restricted to the intertidal, number of days fishing are limited by appropriate tides.

5.4 Fishing operations and results

5.4.1 Effort and intensity

Numbers of ormer fishermen and diving times constitute fishing effort. Catch and effort data are not well documented. The main conclusion that was made by Forster et al. (1982) regarding catches per unit of fishing effort in Guernsey between 1965 and 1977 was that the numbers of shore gatherers have tended to increase despite a decline in their catches. However, during exceptionally low tide much larger catches are to be expected. Some examples of these catches have been given by Forster et al. (1982): on 2 February 1965 about 400 shore gatherers harvested about 31,000 ormers and on 19 January 1977 about 4,000 shore gatherers harvested about 21,000 ormers. An estimated 25,500 ormers were landed by 7,700 fishermen in Guernsey in 1977, while 7,370 ormers were landed by 3,360 fishermen in 1982 (**Table 6**).

Table 6. Catch and effort data of ormers in Guernsey from 1977 through 1982. (Data from States of Guernsey Sea Fisheries Committee, 1984).

Year	Estimated no. of fishermen	Estimated no. of ormers taken
1977	7,700	25,500
1978	3,600	18,300
1979	6,900	31,200
1980	3,900	9,950
1981	1,000	960
1982	3,360	7,370

5.4.2 Selectivity

Considering the behaviour of ormers and the fishing method and gear, selectivity is perhaps based only on animal size.

5.4.3 Catches

Ormer is a highly prized food fish, generally sold fresh, but also keeps well as a frozen product (Bossy and Culley, 1976; Mottet, 1978). Before the 1973 ban on diving for ormers was imposed in the Channel island of Guernsey, divers landed substantially greater ormer numbers than shore gatherers (**Table 7**). The fear that ormer populations would disappear completely from the shores of Guernsey led to a three-year ban on ormer fishing between 1974 and 1976 (**Table 7**) in the hope that populations might recover.

Table 7. Ormer landings in Guernsey from 1965 through 1984. (Data from States of Guernsey Sea Fisheries Committee, 1984).

Year	Taken by shore gatherers	Taken by divers	Total take
1965	168,000	160,000	328,000
1966	198,00	185,000	383,000
1967	198,00	244,000	442,000
1968	60,000	217,000	277,000
1969	9,000	121,000	130,000
1970	109,000	88,000	197,000
1971	151,000	171,000	322,000
1972	60,000	88,000	148,000
1973	9,000	51,000	60,000
1974	-	-	-
1975	-	-	-
1976	-	-	-
1977	25,500	-	25,500
1978	18,300	-	18,300
1979	31,200	-	31,200
1980	9,950	-	9,950
1981	960	-	960
1982	7,370	-	7,370
1983	4,993	-	4,993
1984	6,787	-	6,787

6. PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

The nature of ormers is such that they can be so easily overfished, that numerous regulations aimed at managing and conserving the resource have been put in place. In the Channel Isles, the ormer fishery is managed by the Sea Fisheries Committee of the Channel Islands (Bossy and Culley, 1976) and in France by the Administration des Affaires Maritimes (Berthou et al., 1985).

6.1.1 Limitation or reduction of total catch

The methods of fishery regulation, aiming at reducing fishing effort are:

(a) Licensing

Ormer fishermen are required to obtain licences. Fishing pressure is decreased by simply restricting the number of licences issued. Bossy and Culley (1976) note that this method is too expensive and difficult to enforce.

(b) Bag limits

Bag limits can effectively reduce fishing pressure, but again is difficult to enforce and it is easy for fishermen to cheat (Berthou et al., 1985).

(c) Closed areas (zoning) and closed seasons

Certain areas may be closed completely, allowing fishing in different areas in different seasons, or within one season. However, this method does little to reduce fishing pressure. This is because more fishing effort (i.e. many shore gatherers) is concentrated during the open seasons or in the open areas.

(d) Restrictions on the fishing method.

As mentioned previously diving and the use of compressed air (SCUBA) to catch ormers is forbidden in the Channel Isles (Bossy and Culley, 1976) and in France (Berthou et al., 1985).

6.1.2 Protection of portions of population

(for closed areas and seasons see 6.1.1)

The basic regulatory measure used to protect the resource is a minimum size limit which can be marketed. The minimum legal size of ormer is about 76 mm in the Channel Isles (Bossy and Culley, 1976) and 80 mm in France (Berthou et al., 1985; Clavier, 1992c).

7. CULTURE

Whilst the demand for ormer meat remains strong, supply from wild fishery has dwindled significantly (Clavier, 1992c), and is unable to meet this demand (Anon., 1992). Several studies have been conducted on the culture of ormer. WFA (1968) reported a successful ormer spawning and rearing operation at Hunterston, UK. The eggs and larvae of the ormer were reared in power station condenser cooling water within the following ranges of hydrographic parameters: temperature 15.9 - 24.7°C; dissolved oxygen 88 - 111% saturation; free residual chlorine up to 0.02 ppm; salinity 32 - 34 ‰. Koike (1978) reared ormers from fertilized eggs to 435 days old juveniles in a laboratory at Brest, France. In a small-scale laboratory study at Guernsey, Hayashi (1982) spawned and raised ormers from fertilized eggs to one year old juveniles. In a more elaborate experimental culture operation at Argenton, Finistère Nord, France, Flassch and Aveline (1984) produced large numbers of juvenile ormers for an ocean ranching programme. In Ireland, the feasibility of raising ormers was investigated by the Shellfish Research Laboratory at Carna in Galway, and successfully produced F_1 and F_2 ormers in a hatchery (Mercer, 1981; LaTouche and Moylan, 1984, 1986). Recently Hjul (1991) reported on a successful ormer hatchery operation on the Channel island of Guernsey. Sea based ongrowing of ormers in cages is being carried out in Ireland (Hensey, 1991; La Touche et al., 1993) and in Jersey (Bossy, 1989, 1990).

7.1 Procurement of stocks

During 1976 and 1977 eighty ormers were obtained from the States of Guernsey Sea Fisheries Committee and introduced into Ireland for breeding at the Shellfish Research Laboratory (LaTouche and Moylan, 1984). In 1975 and 1976 Hayashi (1982) collected adult ormers from the wild and held them in a simple aquarium system. The adult ormers used in the rearing experiments by Koike (1978) and Flassch and Aveline (1984) were collected by diving in Brest Bay in 1973.

Prior to spawning adult ormers are conditioned with water temperatures which are increased from ambient temperature by 1°C every 4 days until it reaches 18°C (Flassch and Aveline, 1984). The average gonad maturation level of broodstock is observed regularly. Individuals are fully ripe after 89 days at 18°C which is equivalent to about 1500°C-day (Flassch and Aveline, 1984) measured as effective accumulative temperature (Uki and Kikuchi, 1984).

7.2 Genetic selection of stocks

Ormers have not been domesticated for long, so reliable genetic strains have yet to be developed (Fallu, 1991). Animals to be used as broodstock are usually collected directly from the wild, but if farm-grown animals are available, they are likely to be more convenient to use, but one would have to guard against too intensive inbreeding.

7.3 Induction of spawning and fertilization

Well conditioned adult ormers have ripe eggs and sperm in their gonads. Various techniques have been employed to induce ormers to spawn. Koike (1978) and Flassch and Aveline (1984) used thermal shock to induce spawning in fully mature adult ormers. They first air-dried the animals for half to one hour, then placed them into bags (individually or in pairs of the same sex) and suspended them in tanks for spawning. The water temperature in the tank was increased 4°C above the water temperature in the conditioning tank (18°C), and animals spawned within 5 to 24 hours (Flassch and Aveline, 1984). Hayashi (1982) induced spawning by exposing the animals to ultraviolet light treated seawater. The practice at the Shellfish Research Laboratory involves exposing ripe brood ormers to a 5 micromolar solution of hydrogen peroxide (H_2O_2) and 2 M tris (hydroxymethyl) -methyl-amine buffer in seawater (Morse et al., 1977), maintained at conditioning temperature

(18°C) (Roberts, 1990; Moylan and Mercer, 1993). The pH of the water is first increased to 9.1 by adding 6.6 ml of 2 M tris for each litre of water in the container. Fifteen minutes after adding the tris, 3 ml of 6% H_2O_2 solution is added for each litre of water in the container. After 2 hours the H_2O_2/tris solution in the containers is discarded and replaced with fresh seawater. Spawning generally takes place within 30 minutes of the H_2O_2/tris being discarded, usually males being the first to start (personal observation).

Flassch and Aveline (1984) estimated quantity of eggs spawned by counting the eggs in three-1ml samples collected with an automatic pipette. They measured sperm concentration with a haemocytometer. The sperm concentration is critical since there must be enough sperm to ensure 100% fertilization but not too many to cause the dissolving of the egg membrane. According to Kikuchi and Uki (1974) a suitable range of final sperm concentration is from 100,000 - 1,730,000 sperm ml^{-1} with 200,000 sperm ml^{-1} being optimum with freshly spawned sperm. Fertilization is achieved by quickly adding sperm to a known concentration of eggs in the spawning tank (Flassch and Aveline, 1984). It is important for fertilization to occur rapidly within a narrow time period as this will synchronize the larval development, and simplify future operations. The fertilized eggs are washed several times to minimize polyspermy and enough placed in the spawning tanks to form a uniform single layer on the bottom (Hayashi, 1982).

7.4 Rearing

Hatchery production

The fertilized eggs either develop in the tank used for spawning or are transferred to a different tank. Flassch and Aveline (1984) raised the fertilized eggs in 1- filtered seawater treated with antibiotics (streptomycin sulphate, 50 mg l^{-1} and penicillin G, 30 mg l^{-1}, or chloramphenicol, 8 mg l^{-1}).

Hatching takes place 13 hours after fertilization at 20°C and during this time the larvae are kept in still water which is not changed at all (Koike, 1978). The trochophore larvae are photosensitive and swim to the surface and the water in the bottom of the tank (containing unfertilized eggs and empty egg cases) is siphoned out and replaced by clean water (Flassch and Aveline, 1984). The larvae remain in the tank for 20 to 30 hours until the operculum is formed and the veliger larvae are capable of retracting into the shell. Larvae are less fragile at this stage and can be concentrated. Each day the larvae are rinsed and transferred to clean containers. Flassch and Aveline (1984) replaced the water completely each morning and 75% was replaced at the end of the day. On the 4th day after hatch out, Flassch and Aveline (1984) put larvae into polyester settlement tanks (2 x 0.5 x 0.35 m) with a white-gel coating for metamorphosis and juveniles remained in these tanks until they were 8 months old. Koike (1978), Hayashi (1982), and Moylan and Mercer (1993) placed collection plates (40 x 40 cm, cut from corrugated transparent pespex sheets) into the tanks at the time of settlement of the larvae, i.e. when the veliger larvae began crawling. The collectors had previously been placed in aerated running seawater for about 10 days to produce a thin growth of benthic diatoms on which the newly settled spat would feed. Diatoms are encouraged to grow on the plates by adding nutrients (sodium nitrate and sodium metasilicate) to the seawater on a daily basis.

Present techniques for induction of settlement in competent abalone larvae can be separated into two categories: (a) settlement caused by diatoms and mucus from juvenile abalone, and (b) settlement caused by red crustose algae or gamma-aminobutyric acid (GABA). Work done in Japan revealed that complete settlement and metamorphosis of competent ***H. discus hannai*** larvae is induced by a substratum covered with encrusting diatoms and mucus secretions from grazing juvenile abalone (Seki and Kan-no, 1981). In the United States, Morse et al. (1979) successfully induced synchronous settlement and metamorphosis of competent ***H. rufescens*** larvae by using a solution of 10^{-6} M GABA, a chemical which they found present in the crustose red algae on which abalone larvae settle.

Hayashi (1982) and Moylan and Mercer (1993) reared the spat on the collectors until they had attained a shell length of at least 4 mm which takes about 3 - 4 months. Koike (1978) found ***Tetraselmis suecica*** (a flagellate) to be very effective as supplemental food for spat. When the spat had reached about 4 mm, Hayashi (1982) transferred them to a nursery system consisting of mesh cages (53 x 53 x 22 cm, mesh 3 mm) with three U-shaped plastic shelters, and kept the cages in flowing aerated seawater. Young ormers are weaned on a variety of seaweeds e.g., ***Palmaria palmata, Ulva lactuca*** and ***Laminaria digitata*** cut into small pieces. ***P. palmata*** produces the best growth rate (Koike, 1978; Flassch and Aveline,1984) but a diet of mixed seaweeds is recommended (Koike et al., 1979; K.-S. Mai, pers. comm.).

The nursery system at the Shellfish Laboratory, Carna, as described by Moylan and Mercer (1993), consists of a raceway made from 3 x 1.7 x 0.6 m PVC coated white polyester fabric ("Fastank") which holds 240 collector plates described earlier. Each tank contains 24 cages made from PVC sewer pipe (40 cm diameter x 30 cm height); the bottom of the cage is covered with 2 mm mesh. Attached to each cage is an airlift pump constructed from 2 cm PVC pipe. These airlift pumps constantly circulate seawater from the bottom of the tank into the cages. The settlement tank receives a constant flow of fresh seawater at a rate of 1 l per min. Spat remain in this system until they reach a shell length of 12-15 mm at which stage they are ready for ongrowing at sea sites or in landbased systems (Moylan and Mercer, 1993).

Growout system

On-growing of hatchery-raised ormer seed to market size is achieved by using three methods (La Touche et al., 1993), namely: (a) tank culture (land-based), (b) off-bottom sea cages, (c) on-bottom sea cages. A suitable site for sea-based on-growing is essential. Important factors to be considered when choosing a sea site include, (i) good water quality, (ii) relatively fast water currents, (iii) availability of adequate food supply, (iv) shelter from rough weather conditions. Ormers under intensive cultivation have to be stocked at optimum densities since stocking density is inversely related to growth rate (Koike et al., 1979; Mgaya and Mercer, 1993).

Bossy (1990) described an on-growing system utilizing modified D-shaped lobster and crab pots covered with

6 mm or 10 mm plastic mesh. Internally these cages were fitted with two layers of shelves made of upturned plastic guttering spaced apart to allow the food to fall between them. Animals grown in this system were fed once per week in summer and once per fortnight in winter. Market size of 65 mm shell length was reached by 50% of the stock in 3.5 years from seed of 10 mm (Bossy, 1990). A summary of the steps involved in the cultivation of ormer is given in **Figure 12**.

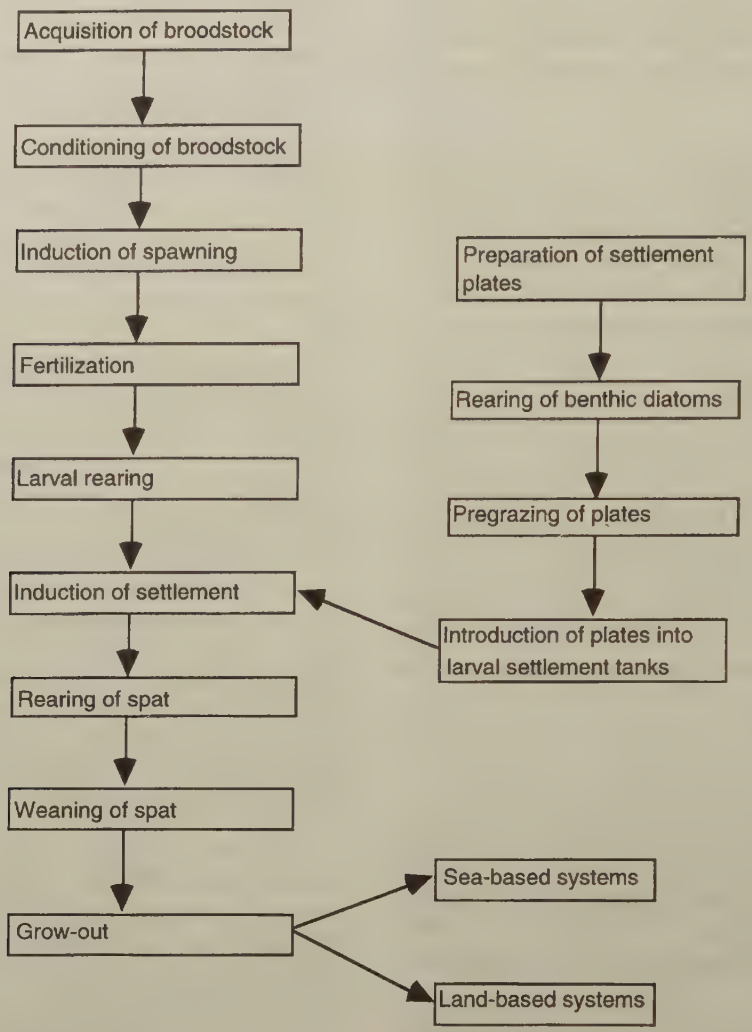

Figure 12. Outline of the steps to culture ***H. tuberculata.***

8. REFERENCES

Abbott, R. T. and Dance, S. P., 1982. Compendium of Seashells. A Colour Guide to More than 4,200 of the World's Marine Shells. New York, E. P. Dutton, Inc., 411 p.

Altman, P. L. and Dittmer, D. S., 1968. Metabolism. Federation of American Societies for Experimental Biology. Bethesda, Maryland, 737 p.

Ambrose, R. F. and Nelson, B. V., 1983. Predation by *Octopus vulgaris* in the Mediterranean. P.S.Z.N.I. *Mar. Ecol.*, 4:251-261.

Anon., 1992. Farmed abalone is needed to fill supply gaps. *Fish Farm. Int.*, 19(11):3

Arai, K., and Wilkins, N. P., 1986. Chromosomes of *Haliotis tuberculata* L. *Aquaculture*, 58:305-308

Barash, A. and Danin, Z., 1992. Fauna Palestina. Mollusca 1. Annotated List of Mediterranean Molluscs of Israel and Sinai. Jerusalem, Israel Academy of Sciences and Humanities, 405 p.

Berthou, P., Beurier, J. P., Buestel, D., and Clavier, J., 1985. Etat actuel des connaissances sur les stocks naturels d'ormeaux: Elements halieutiques et juridiques. *Pêche marit.*, 64(1286):288-294

Bolognari, A., 1953. Ricerche sulla sessualita di *Haliotis lamellosa* Lam. *Arch. zool. ital.*, 38:361-402.

Bossy, S. F., 1989. Provisional results of ormer *(Haliotis tuberculata)* ongrowing trials in cages off Jersey, Channel Islands. *Spec. Publ. Eur. Aquacult. Soc.*, 10:41-42

_____, 1990. Ongrowing of the ormer *Haliotis tuberculata* in Jersey, Channel Islands. *Spec. Publ. Eur. Aquacult. Soc.*, 12:172-173

Bossy, S. F. and Culley, M. B., 1976. Abalone fishing in Britain's Channel Islands. *Fish. News Int.*, 15(9):55-62

Boutan, L., 1899. La cause principale de l'asymétrie des Mollusques gastéropodes. *Arch. Zool. expér. génér.*, (3) 7:203-342.

Brehant, R. N., 1958. Report of Zoology Section,1958. Report and Transactions. *Soc. guernés.*, 16:325

Bruschi, A., Ceppodomo, I., Galli, C. and Piani, P., 1985. Caratterizzazione ecotipologica delle coste italiane. Catalogo dei Molluschi conchiferi viventi nel Mediterraneo. Roma, ENEA, 111 p.

Bryan, G. W., Potts, G. W. and Forster, G. R., 1977. Heavy metals in the gastropod mollusc *Haliotis tuberculata* (L.). *J. mar. biol. Ass. U. K.*, 57:379-390

Bucquoy, E., Dautzenberg, P. and Dollfus, G., 1886. Les Mollusques marins du Roussillon. Tome Ier. Gastropodes. Fascicule XXI. Paris, J. B. Baillière and Fils, pp. 419-454

Clavier, J., 1982. Premières données sur les stocks naturels d'ormeaux de la région de Saint-Malo. Rapport d'etude AMVLCE, 100 p. (Initial data on natural ormer *(Haliotis tuberculata)* stocks in the Saint-Malo region.) Association pour la Mise en Valeur du Littoral de la Cote l'Emeraude. Study report. (Translated from French in *Can. Transl. Fish. Aquat. Sci.*, (1983) 4928:160 p.)

_____, 1983. Etude en vue de l'exploitation des ormeaux dans la région de Saint-Malo, méthodes et résultats préliminaires. *Oceanis*, 9:1-11

_____, 1992a. Fecundity and optimal sperm density for fertilization in the ormer *(Haliotis tuberculata L.)*. In Abalone of the World: Biology, Fisheries and Culture, edited by S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo. Proceedings of the 1st International Symposium on Abalone. Oxford, Fishing News Books, pp. 86-92

_____, 1992b. Infestation on *Haliotis tuberculata* shells by *Cliona celata* and *Polydora* sp. In Abalone of the World: Biology, Fisheries and Culture, edited by S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo. Proceedings of the 1st International Symposium on Abalone. Supplementary Papers. *Fish. Res. Pap. Dep. Fish. (S. Aust.)*, 24:16-20

_____, 1992c. The ormer *(Haliotis tuberculata)* fishery of France and the Channel Islands. In Abalone of the World: Biology, Fisheries and Culture, edited by S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo. Proceedings of the 1st International Symposium on Abalone. Oxford, Fishing News Books, pp. 454-457

Clavier, J. and Chardy, P., 1989. Investigation into the ecology of the ormer (*Haliotis tuberculata* L.), factors influencing spatial distribution. *Aquat. living Resour.*, 2:191-197

Clavier, J. and Richard, P., 1983. Contribution à la connaissance écologique de l'ormeau dans la région de Saint-Malo. *Rapport d'étude AMVLCE,* 143 p.

Clavier, J. and Richard, P., 1984. Etude expérimentale du déplacement de l'ormeau (*Haliotis tuberculata*) dans le milieu naturel. *Rev. Trav. Inst. Pêches marit.*, 46(4):315-326

_____, 1985. Études sur les Ormeaux dans la Région de Saint-Malo, Rapport de synthèse et bibliographie indexée. *Rapport d'étude AMVLCE*, 285 p.

_____, 1986a. Growth of juvenile *Haliotis tuberculata* (Mollusca: Gastropoda) in their natural environment. *J. mar. biol. Ass. U.K.*, 66:497-503

_____, 1986b. Estimation du stock naturel d'ormeaux *(Haliotis tuberculata)* dans la région de Saint-Malo. *Rev. Trav. Inst. Pêches marit.*, 48(3-4):95-105

Cochard, J. C., 1980. Recherches sur les facteurs determinant la sexualité et la reproduction chez *Haliotis tuberculata* L. Thèse présentée à l'Université de Bretagne Occidentale pour l'obtention du doctorat de 31ème cycle, no. 116:167 p. (Research on factors determining sexuality and reproduction in *Haliotis tuberculata* L. Thesis, doctorate, Oceanography, University of Western Brittany. Translated from French in *Can. Transl. Fish. aquat. Sci.*, (1983) 4946:162 p.).

_____, 1982. La croissance de l'ormeau *Haliotis tuberculata* L. en rade de Brest. *Haliotis*,12:61-69

Colombera, D. and Tagliaferri, F., 1983. Chromosomes from male gonads of *Haliotis tuberculata* and *Haliotis lamellosa* (Haliotidae, Archaeogastropoda, Mollusca). *Caryologia*, 36:231-234

Cox, K. W., 1962. California abalones, family Haliotidae. *Calif. Dep. Fish Game Fish Bull.*, (118):1-133

Cox, L. R., 1960. Family Haliotidae Rafinesque, 1815. In Treatise on Invertebrate Paleontology, edited by R. C. Moore. Part I. Mollusca 1. Boulder, Geological Society of America and Lawrence, University of Kansas Press, pp. 221-233

Crofts, D. R., 1929. *Haliotis. Liverpool mar. Biol. Comm. Mem.*, 29:1-174

_____, 1937. The development of *Haliotis tuberculata,* with special reference to organogenesis during torsion. *Phil. Trans. R. Soc. Lond., (B),* 228 (552):219-268, pl. 21-27

_____, 1955. Muscle morphogenesis in primitive gastropods and its relation to torsion. *Proc. zool. Soc. Lond.*, 125:711-750

Croll, R. P., 1983. Gastropod chemoreception. *Biol. Rev.*, 58:293-319

Culley, M. B. and Peck, L. S., 1981. The feeding preferences of the ormer, *Haliotis tuberculata* L. *Kiel. Meeresforsch.*, 5:570-572

Culley, M. and Sherman, K., 1985. The effect of substrate particle size on the production of mucus in *Haliotis tuberculata* L. and the importance of this in a culture system. *Aquaculture*, 47:327-334

D'Angelo, G. and Gargiullo, S., 1978. Guida alle Conchiglie Mediterranee. Milano, Gruppo Editoriale Fabbri, 224 p.

Dauphin, Y., Cuif, J. P., Mutvei, H., and Denis, A., 1989. Mineralogy, chemistry and ultrastructure of the external shell layer in ten species of *Haliotis* with reference to *Haliotis tuberculata* (Mollusca: Archaeogastropoda). *Bull. Geol. Inst. Univ. Uppsala, (n. Ser.)*, 15:7-38

Day, R. W. and Fleming, A. E., 1992. The determinants and measurement of abalone growth. In Abalone of the World: Biology, Fisheries and Culture, edited by S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo. Proceedings of the 1st International Symposium on Abalone. Oxford, Fishing News Books, pp. 141-168

Ebert, E. E., 1969. Abalone. In The encyclopaedia of marine resources, edited by F. E. Firth. New York, Van Nostrand Reinhold Co., pp. 1-4

Emberton, H., 1982. An investigation of the energy budget of the ormer *Haliotis tuberculata* (L.) on different diets and at different temperatures. M.Sc. Thesis, Department of Biological Sciences, Plymouth Polytechnic, Plymouth, UK, 68 p.

Fallu, R., 1991. Abalone Farming. Oxford, Fishing News Books, 202 p.

Flassch, J. P. and Aveline, C., 1984. Production de jeunes ormeaux à la station expérimentale d'Argenton. *Publ. C.N.E.X.O. Rapp. scient. tech.*, (50):68 p.

Fleury, G., 1981. La pêche à pied. Paris, Editions du Pen Duick, 90 p.

_____, 1984. Le pêcheur à pied. Tous les secrets de la marée: Coquillages, poissons et crustacés. Paris, Editions Maritimes et d'Outre-mer, 204 p.

Forster, G. R., 1962. Observations on the ormer population of Guernsey. *J. mar. biol. Ass. U.K.*, 42:493-498

_____, 1967. The growth of *Haliotis tuberculata:* results of tagging experiments in Guernsey 1963-65. *J. mar. biol. Ass. U. K.*, 47:287-300

Forster, G. R., Potts, G. W. and Swinfen, R., 1982. Changes in the ormer populations of Guernsey and Jersey. *J. mar. biol. Ass. U. K.*, 62:717-727

Fretter, Y. and Graham, A., 1962. British prosobranch molluscs: their functional anatomy and ecology. London, Ray Society Publication 144, 755 p.

_____, 1964. Reproduction. In Physiology of Mollusca, vol. 1 edited by K. M. Wilbur and C. M. Yonge. New York, Academic Press, pp. 127-164

_____, 1976. The Prosobranch Molluscs of Britain and Denmark. Part I - Pleurotomariacea, Fissurellacea and Patellacea. *J. moll. Stud.* Suppl. 1:1-37

Gäde, G., 1986. Purification and properties of tauropine dehydrogenase from the shell adductor muscle of the ormer, *Haliotis lamellosa*. *Eur. J. Biochem.*, 160:311-318

_____, 1988. Energy metabolism during anoxia and recovery in shell adductor and foot muscle of the gastropod mollusc *Haliotis lamellosa:* formation of the novel anaerobic end product tauropine . *Biol. Bull.*, 175:122-131

Gaillard, J. M., 1958. *Haliotis tuberculata* Linné. Systématique et distribution. *Bull. Lab. marit. Dinard,* 44:7-11

Gaillard, J. M., 1987. Gastéropodes. In Fiches FAO d'identification des espèces pour les besoins de la pêche, edited by W. Fischer, M.-L. Bauchot and M. Schneider. (Révision 1). Méditerranée et mer Noire. Zone de pêche 37. Volume 1. Végétaux et Invertébrés. Rome, FAO, pp. 513-632

Garavelli, C. L., 1968a. Le *Haliotis* della Provincia Lusitanica. *Conchiglie,* 4(5-6):93-115

_____, 1968b. Postille su *Haliotis tuberculata* ed *Haliotis lamellosa*. *Conchiglie*, 4(7-8):119-120

Gaty, G. and Wilson, J. H., 1986. Effect of body size, starvation, temperature and oxygen tension on the oxygen consumption of hatchery-reared ormers *Haliotis tuberculata* L. *Aquaculture*, 56(3-4):229-237

Girard, A., 1972. La reproduction de l'ormeau, *Haliotis tuberculata* L. *Rev. Trav. Inst. Pêches marit.*, 36(2):163-184

Graham, A., 1988. Molluscs: Prosobranch and Pyramidellid Gastropods. Keys and notes for the identification of species (Second edition). *Synops. br. Fna* (n. Ser.) 2:1-662

Guiry, M. D., 1974. A preliminary consideration of the taxonomic position of *Palmaria palmata* (Linnaeus) Stackhouse = *Rhodymenia palmata* (Linnaeus) Greville. *J. mar. biol. Ass. U.K.*, 54:509-528

Gulland, J. A., 1973. Can a study of stock and recruitment aid management decisions? *Rapp. P.-V. Réun. Cons. Int. Explor. Mer,* 164:368-372.

Habe, T. and Kosuge, S., 1964. A List of the Indo-Pacific Molluscs, concerning to the Japanese Molluscan Fauna. Superfamily Plerotomarioidea. Tokyo, National Science Museum, 8 p.

Hahn, K. O., 1989a. Gonad reproductive cycles. In Handbook of culture of abalone and other marine gastropods, edited by K. O. Hahn. Boca Raton, Florida, CRC Press Inc., pp. 13-39

_____, 1989b. Biotic and abiotic factors affecting the culture of abalone. In Handbook of culture of abalone and other marine gastropods, edited by K. O. Hahn. Boca Raton, Florida, CRC Press Inc., pp.113-134

Hayashi, I., 1977. Investigations into the biology and ecology of the ormer *Haliotis tuberculata* L. Report to the States of Guernsey, 85 p.

_____, 1980a. The reproductive biology of the ormer, *Haliotis tuberculata. J. mar. biol. Ass. U.K.*, 60:415-430

_____, 1980b. Structure and growth of a shore population of the ormer, *Haliotis tuberculata. J. mar. biol. Ass. U.K.,* 60:431-437

_____, 1982. Small scale laboratory culture of the ormer, *Haliotis tuberculata. J. mar. biol. Ass. U.K.*, 62:835-844

_____, 1983. Seasonal changes in condition factors and in the C:N ratio of the foot of the ormer, *Haliotis tuberculata. J. mar. biol. Ass. U.K.*, 63:85-95

Hensey, J., 1991. Abalone. *Aquacult. Ir.*, 49:28

Hjul, P. 1991, Abalone farmer has hatchery in front garden. *Fish Farm. Int.*, 18(11):24-25

Hourquet, H., 1975. Quelques techniques de la pêche à pied. In La pêche à pied en Basse-Normandie, edited by C.R.E.P.A.N. Caen, Comité Régional d'Etude pour la Protection et l'Aménagement de la Nature en Basse-Normandie, pp. 65-74

Jeffreys, J. G., 1865. British Conchology, or an account of the Mollusca which now inhabit the British Isles and the surrounding seas. Volume III. Marine shells, comprising the remaining Conchifera, the Solenoconchia, and Gastropoda as far as *Littorina.* London, Van Voorst, 394 p.

Kaufmann, K. W., 1981. Fitting and using growth curves. *Oecologia (Berl.)*, 49:293-299

Kessel, E., 1935. Über den bau der *Haliotis* - schale. *Zool. Anzeiger.*, 112:290-329

Kikuchi, S. and Uki, N., 1974. Technical study on artificial spawning of abalone, genus *Haliotis* III. Reasonable sperm density for fertilization. *Bull. Tohoku reg. Fish. Res. Lab.*, 34:67-71

Koike, Y., 1978. Biological and ecological studies on the propagation of the ormer, *Haliotis tuberculata* Linnaeus. I: Larval development and growth of juveniles. *La Mer*, 16(3):124-136

Koike, Y., Flassch, J. and Mazurier, J., 1979. Biological and ecological studies on the propagation of the ormer, *Haliotis tuberculata* Linnaeus. II: Influence of food and density on the growth of juveniles. *La Mer,* 17(1):43-52

LaTouche, B. and Moylan, K., 1984. Abalone farming in Ireland. *Aquacult. Ir.*, 16:12-14

_____, 1986. Abalone. *Aquacult. Ir.*, 28:12-13

LaTouche, B., Moylan, K., and Twomey, W., 1993. Abalone on-growing manual. *Aquacult. Expl.*, 14:39 p.

Lindberg, D. R., 1992. Evolution, distribution and systematics of Haliotidae. In Abalone of the World: Biology, Fisheries and Culture, edited by S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo. Proceedings of the 1st International Symposium on Abalone. Oxford, Fishing News Books, pp. 19-23

Linnaeus, C., 1758. Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Regnum Animale. Holmiae (Stockholm), Laurentius Salvius. Vol. 1, 823 p.

Lissman, H. W., 1945. The mechanism of locomotion in gastropod molluscs I. Kinematics. *J. Exp. Biol.*, 21(1-2):58-69

Mercer, J. P., 1981. Low cost spat production units. Proceedings of the Twelfth Annual Shellfish Conference, 19-20 May, 1981. London, Shellfish Association of Great Britain, pp. 69-78

Mercer, J. P., Mai, K.-S., and Donlon, J., 1993. Comparative studies on the nutrition of two species of abalone, *Haliotis tuberculata* Linnaeus and *Haliotis discus hannai* Ino. I. Effects of algal diets on growth and biochemical composition. *Invert. Reprod. Dev.,* 23(2-3):75-88

Mgaya, Y. D. and Mercer, J. P., 1993. Preliminary studies on the effects of stocking density on biomass and growth of the juvenile ormer, *Haliotis tuberculata.* In Irish-American Technical Exchange on the Aquaculture of Abalone, Sea Urchins, Lobsters and Kelp, edited by M. S. van Patten. Abstracts of an International Workshop. *Connect. Sea Grant Coll. Program,* (CT-SG-93-05):16-17

Minchin, D., 1975. The righting response in haliotids. *Veliger*, 17(3):249-250

Morse, A. D. and Morse, D. E., 1984. Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surface of crustose red algae. *J. Exp. mar. Biol. Ecol.,*75:191-215

Morse, D. E., Duncan, H., Hooker, N., and Morse, A., 1977. Hydrogen peroxide induces spawning in molluscs, with activation of prostaglandin endoperoxide synthetase. *Science*, 196:298-300

Morse, D. E., Hooker, N., Duncan, H., and Jensen, L., 1979. Gamma–aminobutyric acid, a neurotransmitter, induces planktonic abalone larvae to settle and begin metamorphosis. *Science*, 204:407-410

Mottet, M. G., 1978. A review of the fishery biology of abalones. *Wash. Dept. Fish. Tech. Rep.*, (37):81p.

Moylan, K. and Mercer, J. P., 1993. Abalone conditioning, spawning techniques, and nursery systems at the Shellfish Research Laboratory, Carna. In Irish-American Technical Exchange on the Aquaculture of Abalone, Sea Urchins, Lobsters and Kelp, edited by M. S. van Patten. Abstracts of an International Workshop. *Connect. Sea Grant Coll. Program,* (CT-SG-93-05):23-24

Mutvei, H., Dauphin, Y. and Cuif, J. P., 1985. Observations sur l'organisation de la couche externe du test de *Haliotis* (Gastropoda): un cas exceptionel de variabilité minéralogique et microstructurale. *Bull. Mus. natn. Hist. nat., Paris,* (4A) 7:73-91

Newman, G. C., 1969. Distribution of the abalone *(Haliotis midae)* and the effect of temperature on productivity. *Investl Rep. Div. Sea Fish. S. Afr.*, (74):7 p.

Nicklès, M., 1950. Mollusques testacé marins de la Côte occidentale d'Afrique. Manuels Ouest-Africains, Vol. II. Paris, Paul Lechevalier, 269 p.

Nordsieck, F., 1968. Die europäischen Meeres-Gehäuseschnecken (Prosobranchia), Vom Eismeer bis Kapverden und Mittelmeer. Stuttgart, Gustav Fischer Verlag, 273 p.

_____, 1975. Some trips to the Canary Islands. *Conchiglia*, 7:3-22

_____, 1982. Die europäischen Meeres-Gehäuseschnecken (Prosobranchia), Vom Eismeer bis Kapverden und Mittelmeer und erweiterte Auflage. Stuttgart and New York, Gustav Fischer Verlag, 539 p.

OECD, 1978. Multilingual dictionary of fish and fish products. Second edition. London, Farnham, Fishing News Books, 431 p.

Parenzan, P., 1970. Carta d'identità delle conchiglie del Mediterraneo Vol. 1, Gastropodi. Taranto, Bios Taras, 283 p.

Peck, L. S., 1983. An investigation into the growth and early development of the ormer, *Haliotis tuberculata,* L. Ph.D. Thesis (C.N.A.A.), Portsmouth Polytechnic, Portsmouth, UK, 386 p.

_____, 1989. Feeding, growth and temperature in the ormer, *Haliotis tuberculata* (L.). *Prog. Underwat. Sci.,* 14:95-107

Peck, L. S. and Culley, M. B., 1990. Structure and density of *Haliotis tuberculata* populations around the coasts of Jersey, Channel Isles. *J. mar. biol. Ass. U.K.*, 70:67-76

Peck, L. S., Culley, M. B. and Helm, M.M., 1987. A laboratory energy budget for the ormer *Haliotis tuberculata* L. *J. Exp. mar. Biol. Ecol.*, 106(2):103-123

Pilsbry, H. A., 1890. Family Haliotidae. In Manual of Conchology, vol. 12, by G. W. Tryon. Philadelphia, Conchological section Academy of natural Sciences, pp. 72-126

Poore, G. C. B., 1972. Ecology of New Zealand abalones *Haliotis* spp. 1: Feeding. *N. Z. J. mar. freshwat. Res.,* 6:11-22

Poppe, G. T. and Goto, Y., 1991. European Seashells. Volume I (Polyplacophora, Caudofoveata, Solenogastra, Gastropoda). Wiesbaden, Verlag Christa Hemmen, 352 p.

Poutiers, J. M., 1993. Les coquillages comestibles de France. In Coquillages, edited by P. Elziére-Papayanni. Paris, Informations Techniques des Services Vétérinaires Français, pp. 13-102

Prince, J. D., Sellers, T. L., Ford, W. B. and Talbot, S. R., 1987. Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis;* Mollusca: Gastropoda). *J. Exp. mar. Biol. Ecol.*,106:243-263

Ricker, W. E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, (191):1-382

Riedl, R., 1983. Fauna und Flora des Mittelmeeres. Ein systematischer Meeresführer für Biologen und Naturfreunde. Dritte, neubearbeitete und erweiterte Auflage. Hamburg and Berlin, Parey, 836 p.

Roberts, P., 1990. Experiments related to culture of the abalone, *Haliotis tuberculata,* (Linné). M.Sc. Thesis, University College Galway, The National University of Ireland, 86 p.

Sabelli, B., Giannuzzi-Savelli, R. and Bedulli, D., 1990-1992. Catalogo annotato dei Molluschi marini del Mediterraneo. Annotated check-list of Mediterranean marine Molusks. Vol. 1 and 2. Bologna, Libreria naturalistica bolognese, 498 p.

Saila, S.B., Recksiek, C.W.and Prager, M.H., 1988. Basic fishery science programs: A compendium of microcomputer programs and manual of operation. *Dev. Aquacult. Fish. Sci.*, 18:1-230

Seki, T. and Kan-no, H., 1981. Induced settlement of the Japanese abalone, *Haliotis discus hannai,* veliger by the mucous trails of the juvenile and adult abalones. *Bull. Tohoku reg. Fish. Res. Lab.*, 43:29-36

Shepherd, S. A., 1973. Studies on Southern Australian abalone (genus *Haliotis*). I. Ecology of five sympatric species. *Aust. J. mar. freshwat. Res.*, 24:217-257

Shepherd, S. A. and Laws, H. M., 1974. Studies on Southern Australian abalone. II. Reproduction of five species. *Aust. J. mar. freshwat. Res.*, 25:49-62

Shepherd, S. A. and Breen, P. A., 1992. Mortality in abalone: its estimation, variability and causes. In Abalone of the World: Biology, Fisheries and Culture, edited by S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo. Proceedings of the 1st International Symposium on Abalone. Oxford, Fishing News Books, pp. 276-304

Shepherd, S. A., Kirkwood, G. R., and Sandland, R. L., 1982. Studies on Southern Australian abalone (genus *Haliotis*). III. Mortality of two exploited species. *Aust. J. mar. freshwat. Res.*, 33:265-272

Sluczanowski, P. R., 1986. A disaggregate model for sedentary stocks: The case of South Australian abalone. In North Pacific Workshop on stock assessment and management of invertebrates, edited by G. S. Jamieson and N. Bourne. *Can. Spec. Publ. Fish. Aquat. Sci.*, 92:393-401

States of Guernsey Sea Fisheries Committee, 1984. Guernsey ormering statistics 1965-1973, 1977-1984. Committee report of the sea fisheries officer, 15 p.

Stephenson, T. A., 1924. Notes on *Haliotis tuberculata. J. mar. biol. Ass. U. K.*, 13(2):480-495

Tanner, F. L., 1926. Report on the Marine Zoological Section, 1926. Report and Transactions. *Soc. guernés.*, 10:29-34

Thiele, J., 1929. Handbuch der systematischen Weichtierkunde. Erster Teil. Loricata / Gastropoda. I: Prosobranchia (Vorderkiemer). Stuttgart, Gustav Fischer Verlag, 376 p.

Tomita, K., 1967. The maturation of the ovaries of the abalone, *Haliotis discus hannai* Ino in Rebun Island, Hokkaido, Japan. *Sci. Rep. Hokkaido Fish. exp. Stn.*, 7:1-7

Tutschulte, T. C. and Connell, J. H., 1981. Reproductive biology of three species of abalones (*Haliotis*) in southern California. *Veliger*, 23(3): 195-206

Uki, N. and Kikuchi, S., 1984. Regulation of maturation and spawning of an abalone, *Haliotis* (Gastropoda) by external environmental factors. *Aquaculture*, 39: 247-261

Underwood, A. J., 1979. The ecology of intertidal gastropods. *Adv. mar. Biol.*, 16:111-210

Vaught, K. C., 1989. A classification of the living Mollusca. Melbourne, American Malacologists Inc., 195 p.

W.F.A. (Ed.), 1968. The potential of the ormer in marine fish farming, Hunterston 1968. White Fish Authority. Marine Cultivation Unit Trials Record, (15):7 p.

Wagner, R. J. and Abbott, R. T., 1978. Standard catalog of shells. Delaware, American Malacologists Inc. Publishers, 3rd ed, pp. 00-203–00-205

Werner, I., 1993. Experimental evaluation of sand as a barrier to abalone (*Haliotis* spp.) movement. M. Sc. Thesis, University College Cork, The National University of Ireland, 92 p.

This synopsis compiles and reviews the currently available information on the biology, fisheries and cultivation of the ormer, *Haliotis tuberculata*. Topics include taxonomy, morphology, distribution, reproduction, pre-adult and adult stages, food and feeding, growth, movement, population characteristics and various aspects of exploitation and culture. Data and information were obtained from both formal and informal scientific publications, journals, newsletters, reports and theses, as acknowledged in the text.

ISBN 92-5-103694-2 ISSN 0014-5602

9 789251 036945

M-42 V7050E/1/9.95/1700